Analysis of the periodically fragmented environment model : I - Influence of periodic heterogeneous environment on species persistence.

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Abstract

This paper is concerned with the study of the stationary solutions of the equation

$$u_t - \nabla \cdot (A(x)\nabla u) = f(x,u), \quad x \in \mathbb{R}^N,$$

where the diffusion matrix A and the reaction term f are periodic in x. We prove existence and uniqueness results for the stationary equation and we then analyze the behaviour of the solutions of the evolution equation for large times. These results are expressed by a condition on the sign of the first eigenvalue of the associated linearized problem with periodicity condition. We explain the biological motivation and we also interpret the results in terms of species persistence in periodic environment. The effects of various aspects of heterogeneities, such as environmental fragmentation are also discussed.

Contents

1 Introduction

"In the last two decades, it has become increasingly clear that the spatial dimension and, in particular, the interplay between environmental heterogeneity and individual movement, is an extremely important aspect of ecological dynamics."

P. Turchin, *Qualitative Analysis of Movement*[1]

Reaction-diffusion equations of the type

$$u_t = \Delta u + f(u) \quad \text{in } \mathbb{R}^N \tag{1.1}$$

have been introduced in the celebrated articles of Fisher (1937) [24] and Kolmogorov, Petrovsky and Piskunov (1938) [39]. The initial motivation came from

[1] 1998, Sinauer Assoc. Inc., Sunderland, Mass.

population genetics and the scope was to shed light on spatial spreading of advantageous genetic features. The nonlinear reaction term considered there are that of a logistic law of which the archetype is $f(u) = u(1-u)$ or extensions like $f(u) = u(1-u^2)$.

Several years later, Skellam (1951) [49] used this type of models to study biological invasions, *i.e.* spatial propagation of species. With these he succeeded to propose quantitative explanations of observations, in particular of muskrats spreading throughout Europe at the beginning of 20th Century or the early dissemination of birch trees in Great Britain.

Since these pioneering works, this type of equation has been widely used to model spatial propagation or spreading of biological species (bacteria, epidemiological agents, insects, plants, etc). Systems involving this type of equations have also been proposed to model the spread of human cultures (Compare in particular Ammerman and Cavalli-Sforza or Cavalli-Sforza and Feldman [2, 19]).

A vast mathematical literature has been devoted to the *homogeneous* equation (1.1). Of particular interest is to understand the structure of *travelling front solutions* and their stability, as well as *propagation* or spreading properties that this equation exhibits. The former are solutions of the type $u(t,x) = U(x\cdot e - ct)$ for any given direction e ($|e| = 1$, e is the direction of propagation) and $U : \mathbb{R} \to (0,1)$. The latter are related to the fact that starting with an initial datum $u_0 \geq 0$, $u_0 \not\equiv 0$ which vanishes outside some compact set, then $u(t,x) \to 1$ as $t \to +\infty$ and the set where u is, say, close to 1 expands at a certain speed which is the *asymptotic speed of spreading*. The papers of Aronson and Weinberger [3], and of Fife and McLeod [23], in particular, represent two mathematical milestones in the literature.

With the important exception of the works of Gärtner and Freidlin (1979)[28] and Freidlin [25], it is only relatively recently that the questions of travelling fronts and the effects of the medium on the asymptotic speed of propagation have been addressed within the framework of *heterogeneous* extensions of (1.1) (see e.g. [5, 26, 27, 33, 47, 51]).

In ecological modelling or for biological invasions, indeed, the heterogeneous character of the environment plays an essential role. It appears that *even at macroscopic scales*, the medium and its various characteristics are far from homogeneous. In the words of Kinezaki, Kawasaki, Takasu and Shigesada, [38] : "... natural environments are generally heterogeneous. For example, they are usually mosaic of heterogeneous habitats such as forests, plains, marshes and so on. Furthermore, they are often fragmented by natural or artificial barriers like rivers, cultivated fields and roads, etc. Thus growing attention has been paid in recent years to the question of how such environmental fragmentations influence the spreading and persistence of invading species". For recent works on this aspect of ecological modelling, we refer the reader for instance to [32, 34, 36] ; compare also the

references on this model quoted in [38].

A first approximation to heterogeneous environments, therefore, is the so-called *patch model*. In it, one assumes a mosaic of differentiated environments, each of which having a relatively well defined structure which one might consider as homogeneous. This involves an equation with piecewise constant coefficients (compare below). This type of model has been proposed by Shigesada, Kawasaki and Teramoto [48] to study biological invasions in periodic environments and is described in the book [47]. They have modified the Fisher's model (1.1), assuming that the intrinsic growth rate and the diffusion coefficient may vary with patches. Considering a situation where two kinds of patches are arranged alternatively, they have introduced the following equation

$$u_t = (A(x)u_x)_x + u(\mu(x) - u) \quad \text{in } \mathbb{R}, \tag{1.2}$$

where $\mu(x)$ is interpreted as the *intrinsic growth rate* of the population, and where μ and A are piecewise constant, that is

$$\mu(x) = \begin{cases} \mu^+ & \text{in } E^+ \subset [0, L], \\ \mu^- & \text{in } E^- = [0, L] \backslash E^+, \end{cases}$$

and

$$A(x) = \begin{cases} a^+ & \text{in } E^+, \\ a^- & \text{in } E^-; \end{cases}$$

next, $\mu(x)$ and $A(x)$ are extended periodically to $\mathbb{R}$.

Saying that the environment E^+ is more favourable than E^- means that

$$\mu^+ > \mu^-.$$

Thus, regions of space where $\mu(x)$ is relatively high represent favourable zones where the species can develop well. On the contrary, low $\mu(x)$ regions are less favourable to the species.

With the help of numerical experiments on the equation (1.2), Shigesada and Kawasaki [47] found that, depending on the parameter values, the invading species either survives or becomes extinct. Consequently, their first aim was to give a mathematical condition for the species to survive. They empirically proved that the stability of the zero solution of (1.2) was playing a key role ; more precisely, they established that when 0 is a stable solution of (1.2), the population becomes extinct, whereas, in the other case, the population converges to another positive and periodic solution of (1.2).

Thanks to this result, they were able to study the very important ecological issue of the effects of environmental fragmentation on biological conservation. For the one-dimensional patch model, on the basis of numerical computations, they

especially pointed out that, everything else equal, having small unfavourable zones left less chances for survival than having one large zone (with the same total surface). This is a remarkable discovery in this model which sets on a firm theoretical ground the adverse effect of environment fragmentation. A good example to see this is to wonder whether several roads across some forest are better or worse for species survival than one large road with the same total width.

Similar models can also be formulated in higher dimensions. For instance, in dimension two, if $C = [0, L_1] \times [0, L_2]$ ($L_1,\ L_2 > 0$) then one considers the same definitions as above for problem (1.2) with $A(x_1, x_2)$ and $f(x_1, x_2, u)$ being L_1-periodic in x_1 and L_2-periodic in x_2, with (E^+, E^-) being a partition of C which is extended periodically in $\mathbb{R}^2$.

More generally, a *periodic heterogeneous* model is proposed in [47] to investigate the effect of heterogeneity of the environment for more general periodic frameworks. Equation (1.2) is generalized to :

$$u_t - \nabla \cdot (A(x)\nabla u) = f(x, u), \quad x \in \mathbb{R}^N, \tag{1.3}$$

where the diffusion matrix $A(x)$ and the reaction term $f(x, u)$ now depend on the variables $x = (x_1, \cdots, x_N)$ in a periodic fashion, and are not necessarily piecewise constant.

The typical example considered in [38, 47, 48] is

$$f(x, u) = u(\mu(x) - \nu(x)u), \tag{1.4}$$

where $\nu(x)$ reflects a saturation effect related to competition for resources. With $\nu \equiv 1$, one obtains

$$f(x, u) = u(\mu(x) - u), \tag{1.5}$$

which is also widely used in the literature. Moreover, the intrinsic growth rate $\mu(x)$ can actually become negative. In such a region, if isolated from other regions, the species would actually die out. The way the diffusion matrix $A(x)$ depends on x in more or less favourable environments varies from one case to another. As pointed out by Shigesada and Kawasaki [47], certain species, upon arriving in unfavourable environments, speed up (meaning, say in one dimension, that $A(x)$ increases) while the progression of others is hindered (meaning that $A(x)$ decreases).

The periodic patch model considered by Shigesada and Kawasaki is a particular important case of this periodic framework. However, Shigesada and Kawasaki have not generalized their study to this model.

In this paper, we address *the general case* of equation (1.3) (not necessarily piecewise constant) and in higher dimensions as well. The aim of the present work is : (i) to give a complete and rigorous treatment of the mathematical questions which have been raised by Shigesada and Kawasaki [47] and to discuss these types

of problems in the framework of a general periodic environment and in higher dimensions as well ; namely, we obtain existence, uniqueness and stability results for the stationary problem associated to (1.3), and these results conduct to a necessary and sufficient condition for a species to survive, (ii) to study, from a mathematical standpoint, the question of environmental fragmentation. As far as we know, even in the simplified case of the one-dimensional periodic patch model, the results are proved rigorously here for the first time.

The present paper is the first one in a series of two. Here we are chiefly concerned with discussing the existence of a stationary state of (1.3), that is a positive solution $p(x)$ of

$$\begin{cases} -\nabla \cdot (A(x)\nabla p) = f(x,p) \ \text{ in } \mathbb{R}^N, \\ p(x) > 0, \ x \in \mathbb{R}^N. \end{cases} \tag{1.6}$$

Under some assumptions which will be made precise later, solutions of (1.6) may turn out to be periodic. But the periodicity assumptions will not always be made a priori. Periodicity is understood here to mean L_1-periodicity in x_1,..., L_N-periodicity in x_N (assuming that $A(x)$ and $f(x,u)$ have such a dependance in x).

In problems (1.2), (1.3) and (1.6), it is not easy to understand the complex interaction between more favourable and less favourable zones. Furthermore, how does the balance between diffusion and reaction play a role? It is not obvious a priori and it may actually sometimes be counter-intuitive. We establish here a simple necessary and sufficient condition for such a solution of (1.6) to exist. This criterion is related to existing results in the literature [13, 14, 15, 20, 44].

In the ecological context, existence of a solution of (1.6) should be viewed as a condition allowing for the survival of the species under consideration. Thus, within the framework of model (1.3), we obtain a necessary and sufficient condition for the survival of this species in a periodic environment. This point is made precise after the first results of Section 2. Using this criterion, we proceed to discuss various conditions under which the species survives. In particular, we treat the question of the role of fragmentation of the environment. We use here the method of rearrangement.

Results of the same kind have been established in the case of bounded domains with boundary conditions, which is different from the point of view that one has in studying spreading, in a series of papers by Cantrell and Cosner (see in particular [13, 14, 15]), who have also further discussed systems in [16]. We summarize some of their results in Section 6. Furthermore, we show that the method of rearrangement allows us to simplify and generalize many of the known results for bounded domains.

For general equation (1.6), we prove some new Liouville type results of independent mathematical interest. These results will be stated in the next section.

The present paper is organized as follows. In the next section, we set the mathematical framework and state all the main results. Each result is followed by its biological interpretation. In Section 3, we prove uniqueness and existence results for solutions of (1.6). In particular, there we establish a nonlinear Liouville theorem. Next, in Section 4, we give some stability results concerning the long time behaviour of solutions of problem (1.3) with initial data. In Section 5, we apply the general results to some special classes of functions f arising in some biological models, and we state some "species persistence" results. In Section 6, we summarize some facts on the bounded domains case with different types of boundary conditions. Lastly, in Section 7, we conclude this paper with a discussion on the biological implications of this work.

2 Statements of the main results

We are concerned here with equation

$$u_t - \nabla \cdot (A(x)\nabla u) = f(x,u), \quad t \in \mathbb{R}_+, \ x \in \mathbb{R}^N, \tag{2.1}$$

and its stationary solutions given by

$$-\nabla \cdot (A(x)\nabla u) = f(x,u), \quad x \in \mathbb{R}^N. \tag{2.2}$$

Let L_1,...,$L_N > 0$ be N given real numbers. In the following, saying that a function $g : \mathbb{R}^N \to \mathbb{R}$ is periodic means that $g(x_1, \cdots, x_k + L_k, \cdots, x_N) \equiv g(x_1, \cdots, x_N)$ for all $k = 1, \cdots, N$. Let C be the period cell defined by

$$C = (0, L_1) \times \cdots \times (0, L_N).$$

Let us now describe the precise assumptions. Throughout the paper, the diffusion matrix field $A(x) = (a_{ij}(x))_{1 \le i,j \le N}$ is assumed to be periodic, of class $C^{1,\alpha}$ (with $\alpha > 0$), and uniformly elliptic, in the sense that

$$\exists \alpha_0 > 0, \ \forall x \in \mathbb{R}^N, \ \forall \xi \in \mathbb{R}^N, \quad \sum_{1 \le i,j \le N} a_{ij}(x)\xi_i\xi_j \ge \alpha_0 |\xi|^2. \tag{2.3}$$

The function $f : \mathbb{R}^N \times \mathbb{R}_+ \to \mathbb{R}$ is of class $C^{0,\alpha}$ in x locally in u, locally Lipschitz-continuous with respect to u, periodic with respect to x. Moreover, assume that $f(x,0) = 0$ for all $x \in \mathbb{R}^N$, that f is of class C^1 in $\mathbb{R}^N \times [0,\beta]$ (with $\beta > 0$), and set $f_u(x,0) := \lim_{s \to 0^+} f(x,s)/s$. Unless otherwise specified, the assumptions

above are made throughout the paper. In Remark 2.3 below we also explain how to include in our results the case of the patch model which involves terms $f(x,u)$ and $A(x)$ which are discontinuous with respect to x.

In several results below, the function f is furthermore assumed to satisfy

$$\forall x \in \mathbb{R}^N, \quad s \mapsto f(x,s)/s \text{ is decreasing in } s > 0 \tag{2.4}$$

and/or

$$\exists M \geq 0,\ \forall s \geq M,\ \forall x \in \mathbb{R}^N, \quad f(x,s) \leq 0. \tag{2.5}$$

Examples of functions f satisfying (2.4-2.5) are functions of the type (1.4) or (1.5), namely $f(x,u) = u(\mu(x) - \nu(x)u)$ or simply $f(x,u) = u(\mu(x) - u)$, where μ and ν are periodic.

The criterion of existence (as well as uniqueness and asymptotic behaviour) is formulated with the principal eigenvalue λ_1 of the operator $\mathcal{L}_0$ defined by

$$\mathcal{L}_0\phi := -\nabla \cdot (A(x)\nabla\phi) - f_u(x,0)\phi,$$

with periodicity conditions. Namely, we define λ_1 as the unique real number such that there exists a function $\phi > 0$ which satisfies

$$\begin{cases} -\nabla \cdot (A(x)\nabla\phi) - f_u(x,0)\phi = \lambda_1\phi \text{ in } \mathbb{R}^N, \\ \phi \text{ is periodic},\ \phi > 0,\ \|\phi\|_\infty = 1. \end{cases} \tag{2.6}$$

Let us recall that ϕ is uniquely defined by (2.6).

With a slight abuse of definition, in the following we say that 0 is an *unstable solution* of (2.2) if $\lambda_1 < 0$. The stationary state 0 is said to be *stable* otherwise, *i.e.* if $\lambda_1 \geq 0$. These definitions will be seen to be natural in view of the results we prove here.

2.1 Existence and uniqueness results

We are now ready to state the existence and uniqueness result on problem (2.2). Let us start with the criterion for existence.

Theorem 2.1 *1) Assume that f satisfies* (2.5) *and that* 0 *is an unstable solution of* (2.2) (*that is* $\lambda_1 < 0$). *Then, there exists a* positive *and periodic solution p of* (2.2).

2) Assume that f satisfies (2.4) *and that* 0 *is a stable solution of* (2.2) (*that is* $\lambda_1 \geq 0$). *Then there is no positive bounded solution of* (2.2) (*i.e.* 0 *is the only* nonnegative *and bounded solution of* (2.2)).

Remark 2.2 For special nonlinearities f of the type $f(x,u) = u(\mu(x) - \nu(x)u)$, where μ and ν may not be periodic anymore, and for a more general *non-divergence* elliptic operator like $-\nabla \cdot (A(x)\nabla u) + B(x) \cdot \nabla u = f(x,u)$ with drift B, the above results have a probabilistic interpretation. Such equations arise in the theory of branching processes. In this framework, and for nonlinearities $f(x,u) = u(\mu(x) - \nu(x)u)$, Part 1) of Theorem 2.1 is due to Engländer and Pinsky [21] (see also Engländer and Kyprianou [20] and Pinsky [44] and Remark 3.1 below). We are very grateful to J. Engländer, A. Kyprianou and R.G. Pinsky for several useful comments about this literature and on the relationship with the probabilistic point of view.
In the case of bounded domains with Dirichlet, Neumann or Robin boundary conditions, the same type of results as in Theorem 2.1 can be found in [40] (in dimension 1), [13] (in higher dimensions, with constant diffusion) or [14] (with a space and density varying diffusion and a drift term). We refer to Section 6 for more details about the case of bounded domains.

Remark 2.3 We have assumed that $f(x,u)$ was (at least) continuous with respect to x and u. In fact, one can easily extend these results to more general classes of f which cover, in particular, the case of the patch model. The more general statement assumes the following :

(i) $f(x,s)$ is measurable in x and bounded, uniformly on compact sets of $s \in [0, +\infty)$,

(ii) $f(x,s) \leq 0$ for all $s \geq M$, a.e. $x \in \mathbb{R}^n$,

(iii)There is some periodic bounded measurable function $\mu \in L^\infty(\mathbb{R}^n)$ such that $f(x,s) \leq \mu(x)s$ for all $s \in \mathbb{R}$ and a.e. $x \in \mathbb{R}^N$,

(iv) For all $\varepsilon > 0$ there exists $\delta > 0$, such that $f(x,s) \geq \mu(x)s - \varepsilon s$ for all $s \in [0, \delta)$ and a.e. $x \in \mathbb{R}^N$

(v) assumption (2.4) is understood a.e. $x \in \mathbb{R}^N$.

Notice that the eigenvalue problem (2.6) is still well defined. When $s \to f(x,s)$ is C^1, one necessarily must take $\mu(x) = f_u(x,0) \in L^\infty(\mathbb{R}^N)$. Lastly, the assumptions are satisfied by nonlinear terms of the type $f(x,s) = \mu(x)s - \nu(x)s^2$, when $\mu, \nu \in L^\infty(\mathbb{R}^N)$.
Part 2) still holds good if, instead of (2.4), one only assumes that, for any $\beta > 0$, there is $\varepsilon > 0$ such that $f(x,s) \leq f_u(x,0)s - \varepsilon$ for all $x \in \mathbb{R}^N$ and $s \geq \beta$. Part 2) also holds good if, instead of (2.4), the function f is assumed to be such that $f(x,s)/s$ is nonincreasing in $s > 0$ for all $x \in \mathbb{R}^N$, and (strictly) decreasing at least for some x : we would like to thank R.G. Pinsky for pointing out this fact.
In the following, for simplicity, we write the proofs under the more stringent assumptions of the theorem, but the arguments are readily extended to handle this more general framework.

Biological interpretation : As underlined by Shigesada and Kawasaki [47], for an invading species to survive, "the population must increase when rare". Mathematically, this means that the stationary state 0 has to be unstable. In Theorem 2.1, we prove that when 0 is an unstable solution of (1.6), there exists another stationary solution p, which is positive periodic and bounded, and corresponds to a steady state for the invading population. Moreover, Theorem 2.1 also asserts that such a steady state can only exist if "0 is unstable".

Yet, in general, the existence of a positive and bounded steady state p for the invading population does not necessarily guarantee the survival of the species. Indeed, we further have to look at the global stability of this steady state to reach a conclusion about the species survival. Actually, as we will see in Theorem 2.6, this solution p is stable, that is, an initial introduction of the species into a localized region will eventually lead to a stationary pattern in the whole periodic environment through an invasive propagating wave.

Next we state our uniqueness result.

Theorem 2.4 *Assume that f satisfies* (2.4) *and that* 0 *is an unstable solution of* (2.2) *(that is $\lambda_1 < 0$). Then, there exists at most one* positive *and bounded solution of* (2.2)*. Furthermore, such a solution, if any, is periodic with respect to x. If $\lambda_1 \geq 0$ and f satisfies* (2.4)*, then there is no nonnegative bounded solution of* (2.2) *other than* 0*.*

Remark 2.5 The last part of this theorem was already included in Theorem 2.1 above. We repeat it here for the statement to cover both cases $\lambda_1 < 0$ and $\lambda_1 \geq 0$. This theorem is a Liouville type result for problem (2.2). Notice that the solutions of (2.2) are not *a priori* assumed to be periodic in x. The core part in Theorem 2.4 consists in proving that any positive solution of (2.2) is actually bounded from below by a positive constant (see Proposition 3.2 below), which does not seem to be a straightforward property.

Biological interpretation : This Theorem asserts that if a positive and bounded steady state for the population exists, then it is unique. Mathematically, uniqueness in such unbounded domains is much more delicate to prove than in the bounded domains case. It turns out that this property is crucial in the proof of Theorem 2.6. Thus, it is very much related to the global stability of the positive and bounded steady state p, whence to the discussion of the survival of the species.

2.2 Large time behaviour

Let us now consider the parabolic equation (2.1), and let $u(t,x)$ be a solution of (2.1), with initial condition $u(0,x) = u_0(x)$ in $\mathbb{R}^N$. The asymptotic behaviour of

$u(t,x)$ as $t \to +\infty$ is described in the following theorem:

Theorem 2.6 *Assume that f satisfies (2.4) and (2.5). Let u_0 be an arbitrary bounded and continuous function in $\mathbb{R}^N$ such that $u_0 \geq 0$, $u_0 \not\equiv 0$. Let $u(t,x)$ be the solution of (2.1) with initial datum $u(0,x) = u_0(x)$.*

1) If 0 is an unstable solution of (2.2) (that is $\lambda_1 < 0$), then $u(t,x) \to p(x)$ in $C^2_{loc}\left(\mathbb{R}^N\right)$ as $t \to +\infty$, where p is the unique positive solution of (2.2) given by Theorems 2.1, part 1), and 2.4.

2) If 0 is a stable solution of (2.2) (that is $\lambda_1 \geq 0$), then $u(t,x) \to 0$ uniformly in $\mathbb{R}^N$ as $t \to +\infty$.

Remark 2.7 In the above statement, the solution $u(t,x)$ is the (unique) minimal solution of (2.1) with initial condition u_0, in the sense that

$$u(t,x) = \lim_{m \to +\infty} u_m(t,x),$$

where u_m solves (2.1) with initial condition $u_{0,m}$, and the family $(u_{0,m})_{m \in \mathbb{N}}$ is any given nondecreasing sequence of nonnegative, smooth, compactly supported functions which converge to u_0 locally uniformly in $\mathbb{R}^N$. Actually, each $u_m(t,x)$ is itself the limit of $u_{m,n}(t,x)$ as $n \to +\infty$, where $u_{m,n}$ solves

$$(u_{m,n})_t - \nabla \cdot (A(x)\nabla u_{m,n}) = f(x, u_{m,n}), \quad t > 0, \ x \in B_n$$

with initial condition $u_{0,m}$ in B_n and boundary condition $u_{m,n}(t,x) = 0$ for $t > 0$ and $x \in \partial B_n$, where B_n is the open euclidian ball with center 0 and radius n (for n in $\mathbb{N}$ large so that B_n contains the support of $u_{0,m}$). For nonlinearities of the type $f(x,s) = \mu(x)s - \nu(x)s^p$ with $p > 1$, where μ and ν are periodic and $\inf_{\mathbb{R}^N} \nu > 0$, it follows from Theorem 2 of Engländer and Pinsky [22] that this minimal solution u is the unique solution of (2.1) with initial condition u_0. Without the periodicity assumption and with more general non-selfadjoint operators with unbounded coefficients, the subtle question of the uniqueness or nonuniqueness of the solutions of (2.1) with a given initial condition u_0 is discussed in [22].

Let us now consider the particular case $f(x,u) = u(\mu(x) - u)$ for $u \geq 0$, where μ is periodic with respect to x. Such nonlinearities arise in ecological models of species conservation and biological invasions (see section 1 for the motivation and [7, 33] for propagation phenomena related to these equations). Such a function $f(x,u) = u(\mu(x) - u)$ fulfills conditions (2.4) and (2.5). Following Remark 2.3, we may actually relax the regularity assumptions.

Gathering all the previous results, the following corollary holds :

Corollary 2.8 *Let $f(x,u) = u(\mu(x) - u)$ for $u \geq 0$, where μ is in $L^\infty(\mathbb{R}^N)$ and periodic. Let $u_0 \geq 0$, $u_0 \not\equiv 0$ be a bounded and uniformly continuous function in $\mathbb{R}^N$ and let $u(t,x)$ be the solution of (2.1) with initial datum $u(0,x) = u_0(x)$.*

1) If 0 is an unstable solution of (2.2) (that is $\lambda_1 < 0$) then there exists a unique bounded positive *solution p of (2.2), and $u(t,x) \to p(x)$ locally in x as $t \to +\infty$.*

2) If 0 is a stable solution of (2.2) (that is $\lambda_1 \geq 0$), then 0 is the unique nonnegative *bounded solution of (2.2), and $u(t,x) \to 0$ uniformly in $\mathbb{R}^N$ as $t \to +\infty$.*

Biological interpretation : We obtain here a complete description of the asymptotic behaviour of solutions of the evolution equation (1.3). So, Theorem 2.6 helps us to sharpen the informations given by Theorem 2.1. Indeed, Theorem 2.1 asserted that the condition "0 is unstable" is a necessary and sufficient condition for a positive and bounded steady state of the population to exist. Theorem 2.6 says that "0 is unstable" is also a necessary and sufficient condition for an invading species to survive. Besides, Theorem 2.6 justifies the equivalence between "0 is unstable" and $\lambda_1 < 0$.

As underlined by Cantrell and Cosner [14] in the case of bounded domains, having a criterion for persistence expressed in terms of λ_1 offers a major advantage. As a matter a fact, even though the criterion for persistence $\lambda_1 < 0$ has a very simple expression, it reflects many crucial informations regarding the interaction between favourable and unfavourable areas, and also regarding both habitat-dependent rates of movement and habitat-dependent rates of population increase. Note that λ_1 can be numerically calculated, so that the condition for survival can be explicitly evaluated. Moreover, and most important from our point of view, having $\lambda_1 < 0$ as a criterion for species survival allows us to derive several qualitative statements about the effects of the environment's shape on the population as we will see with the next results,. Some of these effects have been studied, with a similar criterion, in a series of papers by Cantrell and Cosner [13, 14, 15] in the case of bounded domains. Compare also Section 6 of this work for extensions.

2.3 Effects of the heterogeneity on species survival

Let us denote by $\lambda_1[\mu]$ the first eigenvalue of (2.6) with $f_u(x,0) = \mu(x)$. From the previous results, we see that, in this model, the survival of the species or its extinction hinge on the sign of $\lambda_1[\mu]$. Furthermore, we show in [7] that this sign also determines biological invasions in the form of travelling front-like solutions (actually *pulsating travelling fronts*). Hence it is of particular interest to investigate how the various factors such as the shape of $\mu(x)$, the distribution of unfavourable zones or large amplitude oscillations in $\mu(x)$, affect the sign of $\lambda_1[\mu]$. The next series of results discuss these effects.

2.3.1 Distribution effects

Let us first discuss the influence of a heterogeneous function μ, that is that μ depends on x, as compared to the case where μ would be constant with the same average.

Proposition 2.9 *Under the above assumptions, one has*

$$\lambda_1[\mu] \leq \lambda_1[\mu_0] = -\mu_0,$$

where $\mu_0 = \dfrac{1}{|C|}\displaystyle\int_C \mu$ *and* $|C|$ *denotes the Lebesgue measure of the cell of periodicity* $C = (0, L_1) \times \cdots \times (0, L_N)$.

Biological interpretation : The result given by Proposition 2.9 has a simple and interesting biological interpretation, since it illustrates that heterogeneity, *in some sense*, can be an advantage in terms of species survival. As an example, let us consider a periodic landscape of fields of corn (each periodicity cell corresponding to a field) that would be attacked by a strictly host-specific insect pest. Assume that the favourableness of this environment for the insect species is proportional to the density of vegetable, and that n vegetables are planted on each field. Proposition 2.9 asserts that an equal share of the n seedlings on the whole area of the field is the worst for the insect survival. The chances of species survival would have been better if, for instance, one would have planted the n seedlings on one half of the field, letting the other half empty.

Let us now study the influence of the repartition of μ, assuming that the distribution function of μ is given.

Let us first discuss the one-dimensional periodic patch model described in the introduction. There, we assume that

$$\mu(x) = \begin{cases} \mu^+ & \text{in } E_+ \subset \mathbb{R}, \\ \mu^- & \text{in } E_- = \mathbb{R} \backslash E_+. \end{cases}$$

Consider now another function $\mu^*(x)$ having the same distribution function as μ but where the unfavourable zone is an interval in any periodicity cell. That is, we set

$$\mu^*(x) = \begin{cases} \mu^+ & \text{in } E_+^* \subset \mathbb{R}, \\ \mu^- & \text{in } E_-^* = \mathbb{R} \backslash E_+^*, \end{cases}$$

with μ^* being L-periodic, as is μ, and $E_-^* \cap (0, L)$ is a (connected) interval. The question we want to solve is to know which of the two configurations leaves most chances for survival.

Proposition 2.10 *With the above notations, assuming that the diffusion coefficient $A(x)$ is a constant positive real number, one has*

$$\lambda_1[\mu^*] \leq \lambda_1[\mu].$$

Biological interpretation : Following the metaphor of Shigesada and Kawasaki [47], one can think of a forest in which a periodic array of parallel roads are cut through. The forest is thought of as a favourable homogeneous medium and roads as an unfavourable homogeneous medium with a constant negative growth rate $\mu_- < 0$. The question here is to know whether several small forest roads, say of widths l_1,...,l_p, in a given periodicity cell, are better –in the sense of species survival– than one big road of width $l_1+\cdots+l_p$. Relying on numerical calculations, Shigesada and Kawasaki [47] have observed that the latter leaves more chances for species survival (see also Section 6 for a discussion on such results with other boundary conditions). Here, we actually prove this result rigorously.

For an initial configuration μ of the favourable and unfavourable areas, μ^* corresponds to the configuration where the whole unfavourable zone is concentrated on an interval (by sliding the periodicity cell by $L/2$, one can also say that the whole favourable zone is concentrated on an interval).

Our result proves that whenever μ allows for survival, so does μ^* but in some cases, μ^* will allow for survival while μ will not. It is indeed simple to construct examples where $\lambda_1[\mu^*] < 0 < \lambda_1[\mu]$.

We actually prove a much more general result, in arbitrary dimension, and for general reaction terms $f(x,u)$. The previous proposition is a particular case of it.

To state our result, we need to introduce the notion of Schwarz and Steiner periodic symmetrizations of a function. For more details and properties about these notions, we refer the reader to the monograph of B. Kawohl [37].

Consider a L-periodic function $\mu(x)$ defined on the real line $\mathbb{R}$. There exists a unique function $\mu^*(x)$, L-periodic on $\mathbb{R}$, satisfying the following properties :

(i) μ^* is symmetric with respect to $x = L/2$ and μ^* is nondecreasing on $[0, L]$ away from the symmetry center $L/2$, i.e.

$$\text{for all } x, y \in [0, L], \quad \mu^*(x) \leq \mu^*(y) \text{ if } |x - L/2| \leq |y - L/2|$$

(ii) μ^* has the same distribution function as μ, that is :

$$\text{meas } \{x \in (0, L);\ \mu(x) \leq \alpha\} = \text{meas } \{x \in (0, L);\ \mu^*(x) \leq \alpha\}$$

for all real α.

This function μ^* is called the Schwarz periodic rearrangement. An example of it is given in Figure 1.

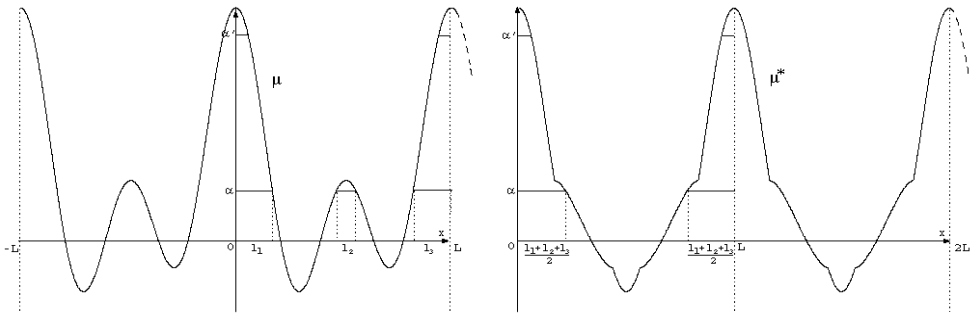

Figure 1: A function μ and its periodic Schwarz rearrangement μ^*

Consider now a function $\mu(x)$ periodic in $\mathbb{R}^N$ with a period cell $C = (0, L_1) \times \cdots \times (0, L_N)$. Keeping fixed all other variables but x_k, we can rearrange as above the function $\mu(x)$ with respect to x_k. This is called Steiner periodic rearrangement in the variable x_k. By performing such Steiner periodic rearrangements successively on all variables $x_1, x_2, \ldots, x_N$, we obtain a new function, $\mu^*(x_1, \cdots, x_N)$. Thus, this function is periodic in all variables, symmetric with respect to each variable x_k, and nonincreasing with respect to each variable x_k for $x_k \in [0, L_k/2]$.

Theorem 2.11 *Assume that the diffusion matrix A is the identity matrix and denote by $\lambda_1[f_u(x,0)]$ the principal eigenvalue of* (2.6) *involving $f_u(x,0)$. Let $f_u^*(\cdot,0)$ be the successive Steiner symmetrizations of $f_u(\cdot,0)$ in the variables $x_1, \ldots, x_N$.*

Then,

$$\lambda_1[f_u^*(\cdot,0)] \leq \lambda_1[f_u(\cdot,0)].$$

Biological interpretation : As already pointed out, this covers the case of the patch model. Even in this case, in higher dimension, say $N = 2$, this property is new. An example of how unfavourable zones are assembled by Steiner rearrangement is described in Figure 2.

Theorem 2.11 shows that the μ^* configuration, where the unfavourable zones are concentrated, leaves better survival chances. In the configuration μ^*, in each direction, the more unfavourable an area is, the closer it is to the center of the periodic cell. Note that the result of the succession of Steiner symmetrizations will depend on the order in which the variables are taken. This result supports the adverse effect of fragmentation of the environment on species persistence. It holds not only in the periodic patch model when $\mu(x)$ takes two values, but for an arbitrary function $\mu(x)$ (also one taking several values). Note, however, that,

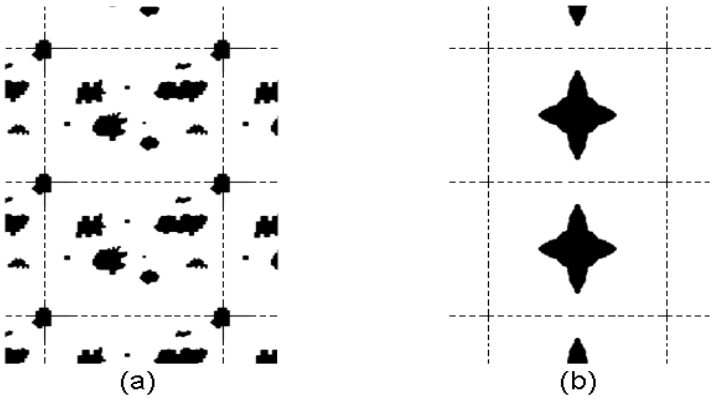

Figure 2: The effect of Steiner symmetrization on unfavourable zones. Distribution of unfavorable zones: (a) for $\mu(x)$ and (b) for rearranged $\mu^*(x)$ successively in the variables x_1 and x_2.

even in the patch model, for a given total area of unfavourable environment in one periodicity cell, the/an optimal shape (i.e. the/a $\widehat{\mu}$ that minimizes $\lambda_1[\mu]$) is not known. However, thanks to Theorem 2.11, we know that there exists an optimal shape which is stable by Steiner symmetrization ($\widehat{\mu}^* = \widehat{\mu}$). It could actually be like in figure 3. We think that it is an interesting open problem to determine the optimal shapes and to derive their properties.

2.3.2 Effects of the amplitude of the heterogeneity

The following result is concerned with the study of the influence of the size of the nonlinearity f. To stress this effect, we now call $\lambda_1(f)$ the first eigenvalue of (2.6) with the nonlinearity f.

Consider the problem

$$-\nabla \cdot (A(x)\nabla u) = Bf(x,u) \text{ in } \mathbb{R}^N, \tag{2.7}$$

where $B > 0$ is a given positive real number and f satisfies assumptions (2.4) and (2.5). As it follows from Theorems 2.1 and 2.4, this problem admits a positive periodic solution if and only if 0 is an unstable solution of (2.7). Let us examine the effect of the amplitude factor B. The following theorem below holds for general functions f :

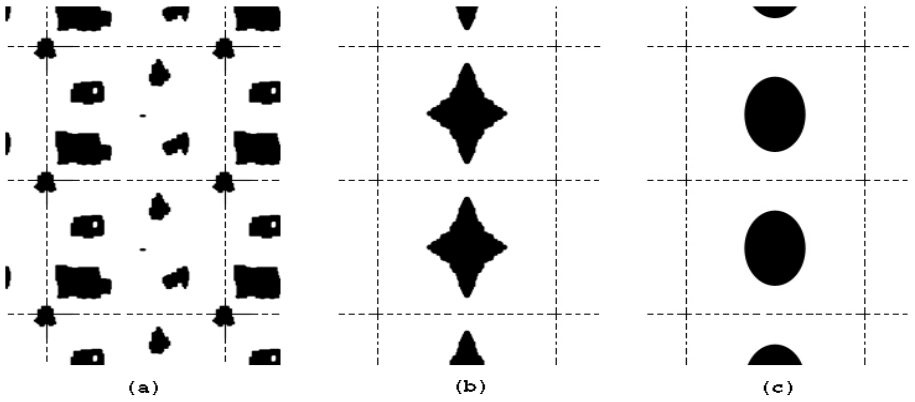

Figure 3: (a) Initial distribution $\mu(x)$, (b) rearranged $\mu^*(x)$ successively in the variables x_1 and x_2, (c) an example of a rearrangement $\widehat{\mu}$, which has the same distribution function as μ and μ^*, and is Steiner symmetric in both variables but is not obtained by the procedure described here.

Theorem 2.12 *1) If* $\int_C f_u(x,0) > 0$, *or if* $\int_C f_u(x,0) = 0$ *and* $f_u(x,0) \not\equiv 0$, *then* $\lambda_1(Bf) < 0$ *for every* $B > 0$, *and the function* $B \mapsto \lambda_1(Bf)$ *is decreasing in* $B \geq 0$.

2) If $\int_C f_u(x,0) < 0$, *then* $\lambda_1(Bf) > 0$ *for all* $B > 0$ *small enough. Assume that there exists* $x_0 \in C$ *such that* $f_u(x_0,0) > 0$. *Then* $\lambda_1(Bf) < 0$ *for* B *large enough, and the function* $B \mapsto \lambda_1(Bf)$ *is decreasing in* B *for* B *large enough.*

Likewise, if we assume that f has a dependence with respect to one parameter B –we write $f = f^B$– such that $f_u^B(x,0) = h(x) + Bg(x)$ for some $h, g \in L^\infty$ and assuming that $g > 0$ on some set of positive measure, we can prove the following. For large B (no matter how h and g are distributed), there is always survival. The proofs are the same as for Theorem 2.12 and will not be detailed separately.

Remark 2.13 For the nonlinear elliptic eigenvalue problem

$$-a_{jk}\partial_{jk}\phi + a_i\partial_i\phi = \lambda m\phi, \tag{2.8}$$

in a bounded domain, with Neumann boundary conditions, and for a given real-valued weight function m, some existence results of eigenvalues having positive eigenfunction have been obtained by Senn and Hess [46], Senn [45] and Brown and

Lin [12] (the last reference concerns the Laplace operator, with either Neumann or Dirichlet conditions).

For time-periodic eigenvalue problems of the type

$$\omega\partial_t\phi - \rho\Delta\phi - h(x,t)\phi = \lambda\phi,$$

in bounded domains, where ω and ρ are positive constants and h is a continuous function that is periodic in t, the dependence of the first eigenvalue λ on the parameters is studied in Hess [31] and Hutson, Mischaikow and Polacik [35].

Biological interpretation : As a consequence of the last theorem, we can say that increasing the amplitude of heterogeneity, assuming that the favourable region is not empty, enhances the chance of having 0 unstable. Hence, it increases the chance of biological survival (existence of a positive solution p of (2.2)). In our forthcoming paper [7], we show that it also increases the speed of biological invasion.

The second part of Theorem 2.12 means that, if in an initial environment, the invading population becomes extinct, then it would suffice to have a favourable zone, even quite small, to guarantee the survival of the species by increasing the amplitude of favourableness and unfavourableness of the environment. For instance, let us consider a periodic environment of fields with two kind of vegetal species, the species A being favourable for an invading insect population, and the species B being unfavourable (one can imagine that it is toxic for the insect, or unfavourable for other reasons). Assume that, initially (i.e. with very few vegetal species), the environment does not let the insect population survive. Theorem 2.12, part 2), asserts that increasing sufficiently the favourableness and unfavourableness of the environment, for instance by spreading some fertilizer will lead to the insect survival (and spreading).

Although increasing the size of the heterogeneity is beneficial, the increase of the frequency is not. Mathematically, the role of the amplitude (B in Theorem 2.12), with respect to the inequality $\lambda_1 < 0$, may be similar to that of the period (say L if the periodicity cell is a square). In other words, a rise in frequency may have the same effect as a reduction of the amplitude, and will lead to weaker chances of survival. As an example, assume that we consider, in the one-dimensional case, a population for whom the intrinsic growth rate is given by $\mu(x) = a + b\sin(2\pi x/l)$, where $a < 0$, $b > 0$, $l > 0$ are three constants. From Theorem 2.12, part 2), for a fixed value of the period l, and a small value of the amplitude b, the population becomes extinct ($\lambda_1 \geq 0$). Similarly, for the reasons that have been mentioned above, for a fixed value of b, a small value of l (high frequency) does not allow the species survival (indeed, with the notations of Theorem 2.12, $\lambda_1\left(f(x/l)\right) = 1/l^2\lambda_1\left(l^2 f(x)\right) \to a$ as $l \to 0$). On the other hand, for a fixed period l, a high value of b leads to species survival.

3 Existence and uniqueness of a stationary solution

We start with existence which is a simpler aspect here.

3.1 Proof of existence

Assume first that 0 is an unstable solution of (2.2) and that condition (2.5) is fulfilled. Let us prove that there exists a positive and periodic solution of (2.2). Let ϕ be the unique positive solution of

$$\begin{cases} -\nabla \cdot (A(x)\nabla\phi) - f_u(x,0)\phi = \lambda_1\phi \ \text{ in } \mathbb{R}^N, \\ \phi \text{ is periodic, } \phi > 0, \ \|\phi\|_\infty = 1, \end{cases} \tag{3.1}$$

with $\lambda_1 < 0$. Since $f(x,u)$ is of class C^1 in $\mathbb{R}^N \times [0,\beta]$ (with $\beta > 0$), for $\kappa > 0$ small enough, one gets:

$$f(x,\kappa\phi) \geq \kappa\phi f_u(x,0) + \frac{\lambda_1}{2}\kappa\phi \ \text{ in } \mathbb{R}^N. \tag{3.2}$$

Therefore, it follows that

$$-\kappa\nabla \cdot (A(x)\nabla\phi) - f(x,\kappa\phi) \leq \frac{\lambda_1}{2}\kappa\phi \leq 0 \ \text{ in } \mathbb{R}^N, \tag{3.3}$$

and $\kappa\phi$ is a subsolution of (2.2) with periodicity conditions. Moreover, if M is taken as in (2.5), the constant M is an upper solution of (2.2) with periodicity conditions, and (for κ small enough) $\kappa\phi \leq M$ in $\mathbb{R}^N$. Thus, it follows from a classical iteration method that there exists a periodic classical solution p of (2.2) which satisfies $\kappa\phi \leq p \leq M$ in $\mathbb{R}^N$. Theorem 2.1, part 1) is proved.

Next, assume that p is a nonnegative bounded solution of (2.2) and assume that 0 is stable ($\lambda_1 \geq 0$). Let ϕ be the first eigenfunction of (3.1). From hypothesis (2.4), one has $f(x,\gamma\phi(x)) < f_u(x,0)\gamma\phi(x)$ for all $x \in \mathbb{R}^N$ and $\gamma > 0$. Hence,

$$-\nabla \cdot (A(x)\nabla(\gamma\phi)) - f(x,\gamma\phi) > \lambda_1\gamma\phi \geq 0 \text{ in } \mathbb{R}^N \tag{3.4}$$

for all $\gamma > 0$.

Recall that p is a nonnegative and bounded solution of (2.2). Since ϕ is bounded from below away from 0 and p is bounded, one can define

$$\gamma^* = \inf\left\{\gamma > 0, \ \gamma\phi > p \text{ in } \mathbb{R}^N\right\} \geq 0. \tag{3.5}$$

Assume that $\gamma^* > 0$, and set $z := \gamma^*\phi - p$. Then $z \geq 0$, and there exists a sequence $x_n \in \mathbb{R}^N$ such that $z(x_n) \to 0$ as $n \to +\infty$.

Assume at first that up to the extraction of some subsequence, $x_n \to \overline{x} \in \mathbb{R}^N$ as $n \to +\infty$. By continuity, $z(\overline{x}) = 0$. As $\gamma^*\phi$ is a supersolution of (2.2) (in the sense that it satisfies (3.4)) with periodicity conditions, it is easy to see from the strong elliptic maximum principle that $z \equiv 0$. Therefore $p \equiv \gamma^*\phi$ is a positive and periodic solution of (2.2). Since $\lambda_1 \geq 0$ (0 is assumed to be stable), it follows from (2.2) and (3.4) that

$$0 = -\nabla \cdot (A(x)\nabla p) - f(x, p(x)) > 0.$$

One is thus led to a contradiction.

In the general case, let $(\overline{x}_n) \in \overline{C}$ be such that $x_n - \overline{x}_n \in \prod_{i=1}^N L_i\mathbb{Z}$. Then, up to the extraction of some subsequence, one can assume that there exists $\overline{x}_\infty \in \overline{C}$ such that $\overline{x}_n \to \overline{x}_\infty$ as $n \to +\infty$. Next, set $\phi_n(x) = \phi(x + x_n)$ and $p_n(x) = p(x + x_n)$. Since both A and f are periodic with respect to x, the functions $\gamma^*\phi_n$ and p_n satisfy

$$\begin{array}{r} -\nabla \cdot (A(x + \overline{x}_n)\nabla(\gamma^*\phi_n)) - f(x + \overline{x}_n, \gamma^*\phi_n) > 0 \\ -\nabla \cdot (A(x + \overline{x}_n)\nabla p_n) - f(x + \overline{x}_n, p_n) = 0 \end{array} \text{ in } \mathbb{R}^N. \tag{3.6}$$

From standard elliptic estimates, it follows that (up to the extraction of some subsequences) p_n converge in C^2_{loc} to a function p_∞ satisfying

$$-\nabla \cdot (A(x + \overline{x}_\infty)\nabla p_\infty) - f(x + \overline{x}_\infty, p_\infty) = 0 \text{ in } \mathbb{R}^N, \tag{3.7}$$

while the sequence $(\gamma^*\phi_n)$ converges to $\gamma^*\phi_\infty := \gamma^*\phi(\cdot + \overline{x}_\infty)$, and

$$-\nabla \cdot (A(x + \overline{x}_\infty)\nabla(\gamma^*\phi_\infty)) - f(x + \overline{x}_\infty, \gamma^*\phi_\infty) > 0 \text{ in } \mathbb{R}^N. \tag{3.8}$$

Let us set $z_\infty(x) := \gamma^*\phi_\infty(x) - p_\infty(x)$. Then

$$z_\infty(x) = \lim_{n \to +\infty} \left[\gamma^*\phi(x + x_n) - p(x + x_n)\right],$$

whence $z_\infty(x) = \lim_{n\to+\infty} z(x+x_n)$. Therefore $z_\infty \geq 0$ and $z_\infty(0) = 0$. It then follows from the strong maximum principle that $z_\infty = 0$ and reaches a contradiction as above.

Finally, in all the cases, one has $\gamma^* = 0$, thus $p \equiv 0$, and the proof of Theorem 2.1 is complete. □

Remark 3.1 Theorem 2.1 holds, as such, if equation (2.2) is replaced by

$$-\nabla \cdot (A(x)\nabla u) + B(x) \cdot \nabla u = f(x, u) \text{ in } \mathbb{R}^N, \tag{3.9}$$

where B is a $C^{0,\alpha}$ periodic drift. Indeed, the proof of Theorem 2.1 does not rely on the variational structure of (2.2).
More generally, consider the case where A, B and f are not periodic (with respect to x) anymore. One can wonder whether a result similar to Theorem 2.1 still holds in this case. For this purpose, a possible generalization of the first eigenvalue λ_1 of the operator $\mathcal{L} = -\nabla \cdot (A(x)\nabla) + B(x) \cdot \nabla - f_u(x,0)$ in $\mathbb{R}^N$ is

$$\begin{aligned} \lambda_1 &= \inf \{\lambda \in \mathbb{R},\ \exists \varphi \in C^2(\mathbb{R}^N) \cap L^\infty(\mathbb{R}^N),\ \varphi > 0,\ (\mathcal{L} - \lambda)\varphi \leq 0 \ \text{ in } \mathbb{R}^N\} \\ &= \inf_{\varphi \in C^2(\mathbb{R}^N) \cap L^\infty(\mathbb{R}^N),\, \varphi > 0} \ \sup_{x \in \mathbb{R}^N} \left(\frac{\mathcal{L}\varphi(x)}{\varphi(x)} \right). \end{aligned}$$

This definition for λ_1 gives the same value as before in the periodic case. With the same arguments as above, one can easily prove that if f satisfies (2.5) and if 0 is an unstable solution of (3.9) ($\lambda_1 < 0$), then there exists a positive solution p of (3.9). On the other hand, if f satisfies (2.4) and if 0 is a strictly stable solution of (3.9) ($\lambda_1 > 0$), then there is no positive bounded solution of (3.9) (i.e. 0 is the only nonnegative and bounded solution of (3.9)). For the proof, assume indeed that there is a positive bounded solution p of (3.9) ; it follows from (2.4) that $\mathcal{L}p \leq 0$, whence $\lambda_1 \leq 0$. However, it is not clear whether, under assumption (2.4), the nonexistence of positive bounded solutions p of (3.9) still holds if $\lambda_1 = 0$. We mention this question as an open problem.
Another possible generalized first eigenvalue of $\mathcal{L}$ in the non-periodic case is the following

$$\begin{aligned} \lambda_1' &= \sup \{\lambda \in \mathbb{R},\ \exists \varphi \in C^2(\mathbb{R}^N),\ \varphi > 0,\ (\mathcal{L} - \lambda)\varphi \geq 0 \ \text{ in } \mathbb{R}^N\} \\ &= \sup_{\varphi \in C^2(\mathbb{R}^N),\, \varphi > 0} \ \inf_{x \in \mathbb{R}^N} \left(\frac{\mathcal{L}\varphi(x)}{\varphi(x)} \right). \end{aligned}$$

In the case of a bounded smooth domain, this definition reduces to the classical first eigenvalue of $\mathcal{L}$ with Dirichlet boundary conditions (see [11], [42]). In the periodic case in $\mathbb{R}^N$, one has $\lambda_1 \leq \lambda_1'$, but with a strict inequality in general, even in the case of constant coefficients (for instance, for $\mathcal{L}u = -u'' + u'$ in $\mathbb{R}$, one has $0 = \lambda_1 < \lambda_1' = 1/4$), see [1], [8], [43]. But this definition of λ_1' is well-suited for a condition on the existence of other types of solutions of (3.9), maybe not bounded, in the general nonperiodic case. Namely, for a function f of the type $f(x,s) = \mu(x)s - \nu(x)s^2$, Pinsky [44] (see also [20]) proved that the existence of a solution of minimal growth at infinity for (3.9) is equivalent to $\lambda_1' < 0$ (a solution of minimal growth at infinity for (3.9) is a positive solution u of (3.9) such that $u \leq v$ in $\mathbb{R}^N \backslash D$ for all bounded domain D and for all nonnegative solution v of (3.9) in $\mathbb{R}^N \backslash D$ with $u \leq v$ on ∂D).

3.2 Proof of uniqueness

For analogous problems on bounded domains with e.g. Dirichlet conditions on the boundary, uniqueness of the positive solutions is well known (compare [4]). The difficulty here arises because of the lack of compactness and because of the fact that one does not assume a priori that u is bounded from below away from zero.

The proof of Theorem 2.4 essentially relies on the following property.

Proposition 3.2 *Assume that* 0 *is an unstable solution of* (2.2). *Let* $u \in C^2\left(\mathbb{R}^N\right)$ *be a bounded nonnegative solution of* (2.2). *Then, either* $u \equiv 0$ *or there exists* $\varepsilon > 0$ *such that* $u(x) \geq \varepsilon$ *for all* $x \in \mathbb{R}^N$.

Note that periodic solutions obviously satisfy this property. But, here, we look at uniqueness within a more general class of functions. In particular, it is not assumed *a priori* that $\inf_{\mathbb{R}^N} u > 0$, which we will now show.

We prove Proposition 3.2 through a succession of lemmas. Let B_R be the open ball of $\mathbb{R}^N$, with centre 0 and radius R. Let y be an arbitrary point in $\mathbb{R}^N$. It is well-known that there exist a unique real number (principal eigenvalue) λ_R^y, and a unique function φ_R^y (principal eigenfunction) in $C^2\left(\overline{B_R}\right)$, satisfying[2]

$$\left\{\begin{array}{rcll} -\nabla\cdot(A(x+y)\nabla\varphi_R^y) - f_u(x+y,0)\varphi_R^y &=& \lambda_R^y\varphi_R^y & \text{in } B_R, \\ \varphi_R^y &>& 0 & \text{in } B_R, \\ \varphi_R^y &=& 0 & \text{on } \partial B_R, \\ \|\varphi_R^y\|_\infty &=& 1. & \end{array}\right. \tag{3.10}$$

Since both λ_R^y and φ_R^y are unique, standard elliptic estimates and compactness arguments imply that the maps $y \mapsto \varphi_R^y$ and $y \mapsto \lambda_R^y$ are continuous with respect to y (the continuity of φ_R^y is understood in the sense of the uniform topology in $\overline{B_R}$). Note that, since f is periodic in x, φ_R^y and λ_R^y are periodic with respect to y as well.

Let $\tilde{\lambda}_1^y$ be the principal eigenvalue and ϕ^y the principal eigenfunction of

$$\left\{\begin{array}{l} -\nabla\cdot(A(x+y)\nabla\phi^y) - f_u(x+y,0)\phi^y = \tilde{\lambda}_1^y\phi^y \text{ in } \mathbb{R}^N, \\ \phi^y \text{ is periodic and positive in } \mathbb{R}^N, \\ \|\phi^y\|_\infty = 1. \end{array}\right. \tag{3.11}$$

First, it is straightforward to observe :

Lemma 3.3 *The first eigenvalue* $\tilde{\lambda}_1^y$ *does not depend on* y. *In other words,* $\tilde{\lambda}_1^y = \lambda_1$ *for all* $y \in \mathbb{R}^N$, *where* λ_1 *is the first eigenvalue of* (2.6).

[2] throughout the paper, the operator ∇ always refers to the derivation with respect to the x variables

Proof. Set $\phi(x) := \phi^y(x-y)$. The function ϕ satisfies

$$\begin{cases} -\nabla\cdot(A(x)\nabla\phi) - f_u(x,0)\phi = \tilde{\lambda}_1^y\phi \text{ in } \mathbb{R}^N, \\ \phi \text{ is periodic and positive in } \mathbb{R}^N, \\ \|\phi\|_\infty = 1. \end{cases} \tag{3.12}$$

Therefore, by uniqueness, one has $\phi = \phi^0$, and $\tilde{\lambda}_1^y = \tilde{\lambda}_1^0 = \lambda_1$. □

Lemma 3.4 *For all $y \in \mathbb{R}^N$ and $R > 0$, one has $\lambda_R^y > \lambda_1$.*

Proof. The function φ_R^y satisfies

$$\begin{cases} -\nabla\cdot(A(x+y)\nabla\varphi_R^y) - f_u(x+y,0)\varphi_R^y & & & \\ \qquad -\lambda_1\varphi_R^y & = & (\lambda_R^y - \lambda_1)\varphi_R^y & \text{in } B_R, \\ \qquad \varphi_R^y & > & 0 & \text{in } B_R, \\ \qquad \varphi_R^y & = & 0 & \text{on } \partial B_R, \\ \qquad \|\varphi_R^y\|_\infty & = & 1. & \end{cases} \tag{3.13}$$

Assume that $\lambda_R^y \le \lambda_1$. Let ϕ^y be the solution of (3.11). Then ϕ^y satisfies

$$\begin{cases} -\nabla\cdot(A(x+y)\nabla\phi^y) - f_u(x+y,0)\phi^y & = & \lambda_1\phi^y & \text{in } B_R, \\ \qquad \phi^y & > & 0 & \text{in } \overline{B_R}. \end{cases} \tag{3.14}$$

Since $\phi^y > 0$ in $\overline{B_R}$, one can assume that $\kappa\varphi_R^y < \phi^y$ in $\overline{B_R}$ for all $\kappa > 0$ small enough. Now, set

$$\kappa^* := \sup\left\{\kappa > 0,\ \kappa\varphi_R^y < \phi^y \text{ in } \overline{B_R}\right\} > 0.$$

Then, by continuity, $\kappa^*\varphi_R^y \le \phi^y$ in $\overline{B_R}$ and there exists x_1 in $\overline{B_R}$ such that $\kappa^*\varphi_R^y(x_1) = \phi^y(x_1)$. But, since $\phi^y > 0$ in $\overline{B_R}$ and $\varphi_R^y = 0$ on ∂B_R, it follows that $x_1 \in B_R$.

On the other hand, the assumption $\lambda_R^y \le \lambda_1$ implies, from (3.13), that

$$-\nabla\cdot(A(x+y)\nabla(\kappa^*\varphi_R^y)) - f_u(x+y,0)\kappa^*\varphi_R^y - \lambda_1\kappa^*\varphi_R^y \le 0 \ \text{ in } B_R.$$

Therefore, it follows from the strong elliptic maximum principle that $\kappa^*\varphi_R^y \equiv \phi^y$ in $\overline{B_R}$, which is impossible because of the boundary conditions on ∂B_R.

Finally, one concludes that $\lambda_R^y > \lambda_1$ (This can also be derived from a characterization in [11]). □

Lemma 3.5 *For all $y \in \mathbb{R}^N$, the function $R \mapsto \lambda_R^y$ is decreasing in $R > 0$.*

Proof. Let R_1 and R_2 be two positive real numbers with $R_1 < R_2$. The proof of this lemma is similar to that of Lemma 3.4, replacing λ_R^y by $\lambda_{R_1}^y$ and λ_1 by $\lambda_{R_2}^y$, and using the fact that $\varphi_{R_2}^y > 0$ in $\overline{B_{R_1}}$. □

The next lemma is a standard result (*see e.g.* [17]), but we include its proof here for the sake of completeness.

Lemma 3.6 *One has* $\lim_{R\to+\infty} \lambda_R^y = \lambda_1$ *uniformly in* $y \in \mathbb{R}^N$.

Proof. For $y \in \mathbb{R}^N$, call $\mathcal{L}^y$ the elliptic operator defined by $\mathcal{L}^y u := -\nabla \cdot (A(x+y)\nabla u) - f_u(x+y,0)u$. Since it is a self-adjoint operator, one has the following variational formula for λ_R^y :

$$\lambda_R^y = \min_{\psi \in H_0^1(B_R),\ \psi \not\equiv 0} Q_R^y(\psi), \tag{3.15}$$

where

$$Q_R^y(\psi) = \frac{\displaystyle\int_{B_R} \left[\nabla\psi \cdot (A(x+y)\nabla\psi) - f_u(x+y,0)\psi^2\right] dx}{\displaystyle\int_{B_R} \psi^2}. \tag{3.16}$$

Choose a family of functions $(\chi_R)_{R\geq 2}$, bounded in $C^2\left(\mathbb{R}^N\right)$ (for the usual norm) independently of R, and such that

$$\begin{cases} \chi_R(x) = 1 \text{ if } |x| \leq R-1, \\ \chi_R(x) = 0 \text{ if } |x| \geq R, \\ 0 \leq \chi_R \leq 1. \end{cases} \tag{3.17}$$

Set $\psi_R = \phi^y \chi_R$ where ϕ^y is the solution of (3.11). Then $\psi_R \in H_0^1(B_R)$ and

$$Q_R^y(\psi_R) = \frac{\displaystyle\int_{B_R} \left[\nabla\psi_R \cdot (A(x+y)\nabla\psi_R) - f_u(x+y,0)\psi_R^2\right] dx}{\displaystyle\int_{B_R} \psi_R^2}. \tag{3.18}$$

Integrating the numerator by parts over B_R, and using the boundary conditions on ∂B_R, one gets

$$Q_R^y(\psi_R) = \frac{\displaystyle\int_{B_R} \left[-\nabla \cdot (A(x+y)\nabla\psi_R)\ \psi_R - f_u(x+y,0)\psi_R^2\right] dx}{\displaystyle\int_{B_R} \psi_R^2}, \tag{3.19}$$

and, by definition of ψ_R,

$$\begin{aligned}
&\int_{B_R} [-\nabla \cdot (A(x+y)\nabla\psi_R)\ \psi_R - f_u(x+y,0)\psi_R^2]dx \\
&= \int_{B_{R-1}} [-\nabla \cdot (A(x+y)\nabla\phi^y)\ \phi^y - f_u(x+y,0)\,(\phi^y)^2]dx \\
&+ \int_{B_R\setminus B_{R-1}} [-\nabla \cdot (A(x+y)\nabla(\phi^y\chi_R))\ \phi^y\chi_R - f_u(x+y,0)(\phi^y\chi_R)^2]dx.
\end{aligned} \tag{3.20}$$

From equation (3.11) satisfied by ϕ^y and using that ϕ^y and χ_R are bounded in $C^2\left(\mathbb{R}^N\right)$, uniformly with respect to y and R, it follows that there exists $C \geq 0$ such that

$$\begin{aligned}
\left| \int_{B_R} \left[-\nabla \cdot (A(x+y)\nabla\psi_R)\ \psi_R - f_u(x+y,0)\psi_R^2\right] dx \right. \\
\left. - \lambda_1 \int_{B_{R-1}} (\phi^y)^2 \right| \ \leq \ CR^{N-1}
\end{aligned} \tag{3.21}$$

for all $R \geq 2$ and $y \in \mathbb{R}^N$. Likewise, one has

$$\left| \int_{B_R} \psi_R^2 - \int_{B_{R-1}} (\phi^y)^2 \right| \leq C' R^{N-1} \tag{3.22}$$

for some $C' \geq 0$, for all $R \geq 2$ and $y \in \mathbb{R}^N$.

But, since each function ϕ^y is continuous, positive and periodic, and since the functions ϕ^y depend continuously and periodically on y (in the sense of the uniform topology in $\mathbb{R}^N$), there exists $\alpha > 0$ such that $\phi^y(x) \geq \alpha$ for all $x \in \mathbb{R}^N$ and $y \in \mathbb{R}^N$. Thus $\displaystyle\int_{B_{R-1}} (\phi^y)^2 \geq \alpha^2 |B_{R-1}|$. Therefore,

$$\frac{\displaystyle\int_{B_R} \psi_R^2}{\displaystyle\int_{B_{R-1}} (\phi^y)^2} \to 1 \text{ as } R \to +\infty, \tag{3.23}$$

uniformly with respect to $y \in \mathbb{R}^N$. Using (3.19), (3.21) and (3.22), one gets that $Q_R^y(\psi_R) \to \lambda_1$ as $R \to +\infty$, uniformly in $y \in \mathbb{R}^N$.

Next, (3.15) and Lemma 3.4 yield $\lambda_1 < \lambda_R^y \leq Q_R^y(\psi_R)$. As a consequence, $\lambda_R^y \to \lambda_1$ as $R \to +\infty$, uniformly in $y \in \mathbb{R}^N$. This completes the proof of Lemma 3.6. $\square$

We are now able to complete the

Proof of Proposition 3.2. Let $u \in C^2\left(\mathbb{R}^N\right)$ be a nonnegative and bounded solution of (2.2). Let us assume that $u \not\equiv 0$. The strong maximum principle then implies that $u > 0$ in $\mathbb{R}^N$.

Since $f(x,u)$ is of class C^1 in $\mathbb{R}^N \times [0,\beta]$ (with $\beta > 0$), since $f(x,0) \equiv 0$ in $\mathbb{R}^N$ and since f is periodic with respect to x, one can choose $\kappa_0 > 0$ small enough such that

$$f(x+y, \kappa\varphi_R^y) \geq \kappa\varphi_R^y f_u(x+y,0) + \frac{\lambda_1}{2}\kappa\varphi_R^y \ \text{ in } B_R, \tag{3.24}$$

for all $0 < \kappa \leq \kappa_0$, $y \in \mathbb{R}^N$ and $R > 0$ (recall that $\lambda_1 < 0$, and $\varphi_R^y > 0$ in B_R).

From Lemmas 3.5 and 3.6, there exists $R_0 > 0$ such that

$$\forall\ R \geq R_0,\ \forall\ y\ \in\ \mathbb{R}^N,\ \lambda_R^y < \frac{\lambda_1}{2} < 0. \tag{3.25}$$

In the sequel, fix some $R \geq R_0$. Set $u^y(x) := u(x+y)$. The function u^y satisfies

$$-\nabla \cdot (A(x+y)\nabla u^y) - f(x+y, u^y) = 0 \ \text{ in } \mathbb{R}^N. \tag{3.26}$$

Furthermore, $\kappa_0\varphi_R^y$ satisfies

$$-\kappa_0\nabla \cdot (A(x+y)\nabla\varphi_R^y) = f_u(x+y,0)\kappa_0\varphi_R^y + \lambda_R^y\kappa_0\varphi_R^y \ \text{ in } B_R. \tag{3.27}$$

Thus, using (3.24) and (3.25), one has

$$-\kappa_0\nabla \cdot (A(x+y)\nabla\varphi_R^y) - f(x+y, \kappa_0\varphi_R^y) \leq (\lambda_R^y - \frac{\lambda_1}{2})\kappa_0\varphi_R^y \leq 0 \ \text{ in } B_R. \tag{3.28}$$

In other words, $\kappa_0\varphi_R^y$ is a sub-solution of (3.26).

Let us now show that $u^y > \kappa_0\varphi_R^y$ in $\overline{B_R}$. If not, there exists $0 < \kappa^* \leq \kappa_0$ and $x_1 \in \overline{B_R}$ such that $\kappa^*\varphi_R^y(x_1) = u^y(x_1)$ and $u^y \geq \kappa^*\varphi_R^y$ in $\overline{B_R}$ (remember that $u^y > 0$ in $\mathbb{R}^N$, whence $\min_{\overline{B_R}} u^y > 0$). Next, since $\varphi_R^y \equiv 0$ on ∂B_R, it follows that $x_1 \in B_R$. On the other hand, the computations above show that the function $\kappa^*\varphi_R^y$ is still a sub-solution of (3.26). The strong maximum principle gives that $\kappa^*\varphi_R^y \equiv u^y$ in $\overline{B_R}$, which is in contradiction with the conditions on ∂B_R.

Finally, one has $u^y > \kappa_0\varphi_R^y$ in $\overline{B_R}$, thus $u^y(0) > \kappa_0\varphi_R^y(0)$. In other words, $u(y) > \kappa_0\varphi_R^y(0)$ for all $y \in \mathbb{R}^N$. Since the function $y \mapsto \kappa_0\varphi_R^y(0)$ is periodic, continuous and positive over $\mathbb{R}^N$, there exists $\varepsilon > 0$ such that $\kappa_0\varphi_R^y(0) > \varepsilon$ for all $y \in \mathbb{R}^N$, and this completes the proof of Proposition 3.2. □

Let us now turn to the

Proof of Theorem 2.4. Let u and $p \in C^2\left(\mathbb{R}^N\right)$ be two *positive* and bounded solutions of (2.2). By Proposition 3.2, there exists $\varepsilon > 0$ such that $u \geq \varepsilon$ and $p \geq \varepsilon$ in $\mathbb{R}^N$.

Therefore, we can define the positive real number

$$\gamma^* = \sup\left\{\gamma > 0,\ u > \gamma p \text{ in } \mathbb{R}^N\right\} > 0. \tag{3.29}$$

Assume that $\gamma^* < 1$, and let us set $z := u - \gamma^* p \geq 0$. From the definition of γ^*, it follows that there exists a sequence $x_n \in \mathbb{R}^N$ such that $z(x_n) \to 0$ as $n \to +\infty$.

Assume first that, up to the extraction of some subsequence, $x_n \to \overline{x} \in \mathbb{R}^N$ as $n \to +\infty$. By continuity, one has $z \geq 0$ in $\mathbb{R}^N$, and $z(\overline{x}) = 0$. Moreover, z satisfies the equation

$$-\nabla \cdot (A(x)\nabla z) - f(x,u) + \gamma^* f(x,p) = 0 \text{ in } \mathbb{R}^N. \tag{3.30}$$

Furthermore, by assumption (2.4), $f(.,s)/s$ is decreasing in $\mathbb{R}_+$ and since we have assume $\gamma^* < 1$, one has $\gamma^* f(x,p) < f(x,\gamma^* p)$. Hence, (3.30) gives

$$-\nabla \cdot (A(x)\nabla z) - f(x,u) + f(x,\gamma^* p) > 0 \text{ in } \mathbb{R}^N. \tag{3.31}$$

Since f is locally Lipschitz continuous in the second variable, one infers from (3.31) that there exists a bounded function b such that

$$-\nabla \cdot (A(x)\nabla z) - bz > 0 \text{ in } \mathbb{R}^N. \tag{3.32}$$

Since $z \geq 0$ and $z(\overline{x}) = 0$, it follows from (3.32) and from the strong maximum principle that $z \equiv 0$, which is impossible because of the strict inequality in (3.32).

In the general case, let $(\overline{x}_n) \in \overline{C}$ be such that $x_n - \overline{x}_n \in \prod_{i=1}^N L_i\mathbb{Z}$. Then, up to the extraction of some subsequence, one can assume that there exists $\overline{x}_\infty \in \overline{C}$ such that $\overline{x}_n \to \overline{x}_\infty$ as $n \to +\infty$. Next, set $u_n(x) = u(x + x_n)$, and $p_n(x) = p(x + x_n)$. Since both A and f are periodic with respect to x, the functions u_n and p_n satisfy

$$\begin{array}{l} -\nabla \cdot (A(x + \overline{x_n})\nabla u_n) - f(x + \overline{x_n}, u_n) = 0 \\ -\nabla \cdot (A(x + \overline{x_n})\nabla p_n) - f(x + \overline{x_n}, p_n) = 0 \end{array} \text{ in } \mathbb{R}^N. \tag{3.33}$$

From standard elliptic estimates, it follows that (up to the extraction of some subsequences) u_n and p_n converge in C^2_{loc} to two functions u_∞ and p_∞ satisfying

$$\begin{array}{l} -\nabla \cdot (A(x + \overline{x_\infty})\nabla u_\infty) - f(x + \overline{x_\infty}, u_\infty) = 0 \\ -\nabla \cdot (A(x + \overline{x_\infty})\nabla p_\infty) - f(x + \overline{x_\infty}, p_\infty) = 0 \end{array} \text{ in } \mathbb{R}^N. \tag{3.34}$$

Moreover, $u_\infty \geq \varepsilon > 0$ and $p_\infty \geq \varepsilon > 0$.

Let us set $z_\infty(x) := u_\infty(x) - \gamma^* p_\infty(x)$. Then $z_\infty \geq 0$ and $z_\infty(0) = 0$. Furthermore, z_∞ satisfies

$$-\nabla \cdot (A(x + \overline{x_\infty})\nabla z_\infty) - f(x + \overline{x_\infty}, u_\infty(x)) + \gamma^* f(x + \overline{x_\infty}, p_\infty(x)) = 0 \text{ in } \mathbb{R}^N. \tag{3.35}$$

Then, arguing as for problem (3.30) above, one obtains a contradiction.

Therefore, we know that $\gamma^* \geq 1$, hence $u \geq p$. By interchanging the roles of u and p, one can prove similarly that $p \geq u$. Furthermore, if p is a positive solution of (2.2), so is the function $x \mapsto p(x_1, \cdots, x_i + L_i, \cdots, x_N)$, for each $1 \leq i \leq N$. Hence, p is periodic. The proof of Theorem 2.4 is complete. □

The same arguments as above lead to the following uniqueness result for a class of solutions of more general elliptic equations with drift terms, under a slightly stronger version of assumption (2.4) :

Theorem 3.7 *Let $A = A(x)$ be a symmetric matrix field satisfying (2.3) and assume that A is of class $C^{1,\alpha}(\mathbb{R}^N)$ and that A and its first-order derivatives are in $L^\infty(\mathbb{R}^N)$. Let B be a vector field of class $C^{0,\alpha}(\mathbb{R}^N) \cap L^\infty(\mathbb{R}^N)$. Let $f : \mathbb{R}^N \times \mathbb{R}_+ \to \mathbb{R}$, $(x, s) \mapsto f(x, s)$ be Lipschitz-continuous in s uniformly in x and assume that $f(\cdot, s)$ is of class $C^{0,\alpha}(\mathbb{R}^N) \cap L^\infty(\mathbb{R}^N)$ locally in s. Assume that*

$$\forall\ 0 < s < s', \quad \inf_{x \in \mathbb{R}^N} \left(\frac{f(x,s)}{s} - \frac{f(x,s')}{s'} \right) > 0.$$

Let u and v be two positive bounded solutions of

$$\begin{cases} -\nabla \cdot (A(x)\nabla u) + B(x) \cdot \nabla u = f(x,u) \\ -\nabla \cdot (A(x)\nabla v) + B(x) \cdot \nabla v = f(x,v) \end{cases} \quad \text{in } \mathbb{R}^N, \tag{3.36}$$

such that $\inf_{\mathbb{R}^N} u > 0$ and $\inf_{\mathbb{R}^N} v > 0$.

Then $u = v$.

Remark 3.8 However, it is not true in general the positive solutions u of (3.36) are bounded from below by a positive constant under the only assumption $\lambda_1 < 0$, where the generalized first eigenvalue λ_1 is defined as in Remark 3.1 above.
Indeed, let f be a Lipschitz-continuous function defined in $[0, 1]$, such that $f(0) = f(1) = 0$, $f > 0$ on $(0, 1)$, $f'(0) > 0$ and $f(s) \leq f'(0)s$ for all $s \in [0, 1]$. It is known (see [39]) that, for any $c \geq 2\sqrt{f'(0)}$, there are positive solutions u of

$$u'' - cu' + f(u) = 0, \quad 0 < u < 1 \ \text{ in } \mathbb{R}$$

with $u(-\infty) = 0$ and $u(+\infty) = 1$. But, under the notations of Remark 3.1, $\lambda_1 = -f'(0) < 0$ in this case.

3.3 Energy of stationary states

This subsection is about an independent result, dealing with the sign of the energy associated to a positive solution of (2.2), under condition (2.4). This result, of independent interest, will be used in the forthcoming paper [7] on propagation phenomena.

Assume in this subsection that there exists a positive and bounded solution p of (2.2) and that condition (2.4) is fulfilled. It then follows from Theorem 2.1, part 2), that 0 is an unstable solution of (2.2) ($\lambda_1 < 0$), and from Theorem 2.4 that such a function p is then unique and periodic. As we have seen, the existence of p is known for instance if $\lambda_1 < 0$ and if condition (2.5) is satisfied (from Theorem 2.1, part 1)).

Consider the energy functional

$$E(u) := \int_C \left\{ \frac{1}{2} \nabla u \cdot (A(x) \nabla u) - F(x,u) \right\} dx, \tag{3.37}$$

defined on

$$H^1_{per} := \left\{ \phi \ \in \ H^1_{loc}(\mathbb{R}^N) \text{ such that } \phi \text{ is periodic} \right\},$$

with $F(x,u) := \displaystyle\int_0^u f(x,s)ds$. We now prove that the energy of p is negative.

Proposition 3.9 *Assume that condition (2.4) is satisfied and that there exists a positive bounded solution p of (2.2). Then $E(p) < 0$.*

Proof. Under the assumptions of Proposition 3.9, let θ be the function defined in $[0,1]$ by

$$\forall\ t \ \in \ [0,1],\ \theta(t) = E(tp) = \int_C \left\{ \frac{1}{2} t^2 \nabla p \cdot (A(x) \nabla p) - F(x, tp(x)) \right\} dx. \tag{3.38}$$

The function θ is of class C^1 and

$$\forall\ t \ \in \ [0,1],\ \theta'(t) = \int_C \left\{ t \nabla p \cdot (A(x) \nabla p) - f(x, tp(x)) p(x) \right\} dx. \tag{3.39}$$

From (2.4) and from the positivity and periodicity of f and p in x, it follows that $f(x, tp(x)) > t f(x, p(x))$ in $\overline{C}$ for all $t \in (0,1)$. Therefore,

$$\forall\ t \ \in \ (0,1),\ \theta'(t) < t \int_C \left\{ \nabla p \cdot (A(x) \nabla p) - f(x, p(x)) p(x) \right\} dx = 0, \tag{3.40}$$

the last equality being obtained by multiplication of the equation (2.2) satisfied by p and integration over C. As a conclusion,

$$E(p) = \theta(1) < \theta(0) = E(0) = 0. \ \square$$

4 The evolution equation

This section is devoted to the

Proof of Theorem 2.6. Assume that f satisfies (2.4) and (2.5). Let u_0 be a non-negative, not identically equal to 0, bounded and uniformly continuous function, and let $u(t,x)$ be the solution of

$$\begin{cases} u_t - \nabla \cdot (A(x)\nabla u) = f(x,u),\ t \in \mathbb{R}_+,\ x \in \mathbb{R}^N, \\ u(0,x) = u_0(x),\ x \in \mathbb{R}^N. \end{cases} \tag{4.1}$$

Assume first that 0 is an unstable solution of (2.2) ($\lambda_1 < 0$). Let $\varphi_R = \varphi_R^0$ be the function satisfying (3.10) with $y = 0$, and call $\lambda_R = \lambda_R^0$. Namely, $\varphi_R \in C^2\left(\overline{B_R}\right)$ and satisfies

$$\begin{cases} -\nabla \cdot (A(x)\nabla \varphi_R) - f_u(x,0)\varphi_R = \lambda_R \varphi_R \text{ in } B_R, \\ \varphi_R > 0 \text{ in } B_R,\ \ \varphi_R = 0 \text{ on } \partial B_R,\ \|\varphi_R\|_\infty = 1. \end{cases} \tag{4.2}$$

From the strong parabolic maximum principle, one has $u(1,x) > 0$ in $\mathbb{R}^N$. Therefore, for $\kappa > 0$ chosen small enough, $\kappa\varphi_R < u(1,x)$ in B_R. Let us extend $\kappa\varphi_R$ to $\mathbb{R}^N$ by setting $v_0(x) := \kappa\varphi_R(x)$ in B_R, and $v_0(x) := 0$ in $\mathbb{R}^N \backslash B_R$. Define the function v_1 by

$$\begin{cases} \partial_t v_1 - \nabla \cdot (A(x)\nabla v_1) = f(x,v_1),\ t \in \mathbb{R}_+,\ x \in \mathbb{R}^N, \\ v_1(0,x) = v_0(x), \quad \text{for} \quad x \in \mathbb{R}^N. \end{cases} \tag{4.3}$$

As it has been done in the course of the proof of Proposition 3.2, using (3.28), for R large enough and $\kappa > 0$ small enough, $\kappa\varphi_R$ is a subsolution of (2.2) in B_R, and therefore v_0 is a "generalized" subsolution of (2.2) in $\mathbb{R}^N$. Thus v_1 is nondecreasing in time t. Furthermore, $v_1(0,x) \le u(1,x)$ in $\mathbb{R}^N$ implies

$$v_1(t,x) \le u(1+t,x) \text{ in } \mathbb{R}_+ \times \mathbb{R}^N. \tag{4.4}$$

Moreover, for $\kappa > 0$ small enough, $v_0(x) \le p(x)$ in $\mathbb{R}^N$, where p is the unique positive, and periodic, solution of (2.2) (the existence and uniqueness of such a p follows from assumptions (2.4), (2.5) and $\lambda_1 < 0$, owing to Theorems 2.4 and 2.1, part 1)). Since p is a stationary solution of (2.1), one has

$$v_1(t,x) \le p(x) \text{ in } \mathbb{R}_+ \times \mathbb{R}^N, \tag{4.5}$$

Because v_1 is nondecreasing in time t, standard elliptic estimates imply that v_1 converges in $C^2_{loc}\left(\mathbb{R}^N\right)$ to a bounded stationary solution $\underline{v_\infty}(\le p)$ of (2.1). Furthermore, one has $\underline{v_\infty}(0) \ge v_1(0,0) \ge \kappa\varphi_R(0) > 0$. Using the strong maximum

principle, it follows that $\underline{v_\infty} > 0$ in $\mathbb{R}^N$, and we infer from Theorem 2.4 that $\underline{v_\infty} \equiv p$.

Next, from (2.5), there exists $M > 0$ such that $f(x,s) \leq 0$ in $\mathbb{R}^N$ for all $s \geq M$ and $x \in \mathbb{R}^N$. Take M large enough so that $M \geq u_0$ in $\mathbb{R}^N$ and let v_2 be defined by

$$\begin{cases} \partial_t v_2 - \nabla \cdot (A(x)\nabla v_2) = f(x, v_2), \ t \in \mathbb{R}_+, \ x \in \mathbb{R}^N, \\ v_2(0,x) = M, \ x \in \mathbb{R}^N. \end{cases} \tag{4.6}$$

Then, since M is a supersolution of (2.2), v_2 is nonincreasing in time t. Besides, since $v_2(0,x) = M \geq u_0(x) \geq 0$ in $\mathbb{R}^N$,

$$v_2(t,x) \geq u(t,x) \geq 0 \text{ in } \mathbb{R}_+ \times \mathbb{R}^N. \tag{4.7}$$

Furthermore, since $v_2 \geq 0$ from the maximum principle, v_2 converges in $C^2_{loc}\left(\mathbb{R}^N\right)$ as $t \to +\infty$ to a bounded and nonnegative stationary solution $\overline{v_\infty} (\leq M)$ of (2.1). From Theorem 2.4, either $\overline{v_\infty} \equiv 0$ or $\overline{v_\infty} \equiv p$. Finally, one has

$$v_1(t,x) \leq u(1+t,x) \leq v_2(1+t,x), \ t > 0 \ x \in \mathbb{R}^N. \tag{4.8}$$

Since $v_1(t,x) \to p(x)$ as $t \to +\infty$, it follows from (4.8) that $\overline{v_\infty} \equiv p$, and that $u(t,x)$ converges to $p(x)$ in $C^2_{loc}\left(\mathbb{R}^N\right)$ as $t \to +\infty$. Part 1) of Theorem 2.6 is proved.

Let us now assume that 0 is a stable solution of (2.2). Then, as carried above, there exists $M > 0$ such that $f(x,s) \leq 0$ for all $s \geq M$ and $x \in \mathbb{R}^N$. Taking M large enough so that $u_0 \leq M$, one again obtains, defining v_2 as above,

$$v_2(t,x) \geq u(t,x) \geq 0 \text{ in } \mathbb{R}_+ \times \mathbb{R}^N. \tag{4.9}$$

But this time, from the result of Theorem 2.1, part 2), v_2 converges in $C^2_{loc}\left(\mathbb{R}^N\right)$ to 0 as $t \to +\infty$. Furthermore, the convergence is uniform in x : indeed, v_2 is periodic in x at each time $t \geq 0$, since it is so at $t = 0$, and equation (2.1) is periodic in x. It follows from (4.9) that $u(t,x)$ converges to 0 uniformly as $t \to +\infty$, and this concludes the proof of Theorem 2.6, part 2). □

5 Conservation of species in ecological systems

In this section, we study various effects of the term $f_u(x,0)$ on the principal eigenvalue λ_1 of (2.6).

5.1 Influence of the "amplitude" of the reaction term

This subsection is devoted to the stability condition of the zero steady state when the nonlinearity f is replaced by Bf in (2.2), where B is a positive real number. Here, the function f is fixed. Let us call $\lambda_1(Bf)$ the first eigenvalue of (2.6) with the nonlinearity Bf, and $\phi_B \in C^2\left(\mathbb{R}^N\right)$ the unique principal eigenfunction (with the normalization condition $\|\phi_B\|_\infty = 1$) of

$$\begin{cases} -\nabla \cdot (A(x)\nabla\phi_B) - Bf_u(x,0)\phi_B = \lambda_1(Bf)\phi_B, \\ \phi_B \text{ is positive and periodic in } \mathbb{R}^N. \end{cases} \tag{5.1}$$

The next two statements are concerned with the dependence of $\lambda_1(Bf)$ with respect to B and correspond to parts 1) and 2) of Theorem 2.12 respectively.

Proposition 5.1 *If* $\displaystyle\int_C f_u(x,0) > 0$, *or if* $\displaystyle\int_C f_u(x,0) = 0$ *and* $f_u(x,0) \not\equiv 0$, *then* $\lambda_1(Bf) < 0$ *for every* $B > 0$ *and the function* $B \mapsto \lambda_1(Bf)$ *is decreasing in* $\mathbb{R}^+$.

Proof. One first shows that the mapping $B \mapsto \lambda_1(Bf)$ is concave. Since the operator $\mathcal{L}u = -\nabla \cdot (A(x)\nabla u) - Bf_u(x,0)$ is self-adjoint, the eigenvalue $\lambda_1(Bf)$ is obtained from the variational characterization:

$$\lambda_1(Bf) = \min_{\phi \in H^1_{per},\ \phi \not\equiv 0} \frac{\displaystyle\int_C \nabla\phi \cdot (A(x)\nabla\phi) - Bf_u(x,0)\phi^2}{\displaystyle\int_C \phi^2}, \tag{5.2}$$

where H^1_{per} was defined in the previous section. Thus, it follows that $B \mapsto \lambda_1(Bf)$ is concave, whence continuous (on $\mathbb{R}$).

Next, integrate equation (5.1) by parts over C. Using the periodicity of ϕ_B, one obtains,

$$-B\int_C f_u(x,0)\phi_B = \lambda_1(Bf)\int_C \phi_B. \tag{5.3}$$

Take an arbitrary sequence $B_n \to 0$. Since $\lambda_1(B_n f) \to \lambda_1(0) = 0$, standard elliptic estimates and Sobolev injections imply, up to the extraction of some subsequence, that the functions ϕ_{B_n} converge to a nonnegative function ψ, locally (and therefore uniformly by periodicity) in $W^{2,p}$ for all $1 < p < \infty$ (we recall that $f_u(x,0)$ is in L^∞). Furthermore, ψ is such that $\|\psi\|_\infty = 1$, ψ is periodic and satisfies

$$-\nabla \cdot (A(x)\nabla\psi) = \lambda_1(0)\psi = 0. \tag{5.4}$$

From the strong maximum principle, ψ is positive and $\psi \equiv \phi_0 \equiv 1$. By a classical argument we can then show that the whole family ϕ_B converges to 1 as $B \to 0$.

Then, divide (5.3) by B and pass to the limit as $B \to 0$, $B \neq 0$. It follows that

$$\left.\frac{d\lambda_1(Bf)}{dB}\right|_{B=0} |C| = -\int_C f_u(x,0), \tag{5.5}$$

where $|C|$ denotes the Lebesgue measure of C.

Assume now that $\displaystyle\int_C f_u(x,0) > 0$. Since $B \mapsto \lambda_1(Bf)$ is concave, $\lambda_1(0) = 0$ and $\left.\frac{d\lambda_1(Bf)}{dB}\right|_{B=0} < 0$, it follows that $\lambda_1(Bf) < 0$ for every positive B and the function $B \mapsto \lambda_1(Bf)$ is decreasing in $\mathbb{R}^+$.

Similarly, if $\displaystyle\int_C f_u(x,0) = 0$, then $\lambda_1(Bf) \leq 0$ for every positive B. Furthermore, dividing equation (5.1) by ϕ_B and integrating over C leads to :

$$\lambda_1(Bf)\ |C| = -\int_C \frac{\nabla\phi_B \cdot \nabla(A(x)\nabla\phi_B)}{\phi_B^2}. \tag{5.6}$$

If $\lambda_1(Bf) = 0$ for some $B > 0$, then ϕ_B is constant, whence $f_u(x,0) \equiv 0$. Therefore, if one further assumes that $f_u(x,0) \not\equiv 0$, then $\lambda_1(Bf) < 0$ for each $B > 0$, and the function $B \mapsto \lambda_1(Bf)$ is decreasing in $\mathbb{R}_+$. This completes the proof of Proposition 5.1. □

In the case $\displaystyle\int_C f_u(x,0) < 0$, we now prove the following result.

Proposition 5.2 *If $\displaystyle\int_C f_u(x,0) < 0$, then $\lambda_1(Bf) > 0$ for all $B > 0$ small enough. If there exists $x_0 \in C$ such that $f_u(x_0,0) > 0$, then, for B large enough, $\lambda_1(Bf) < 0$ and $\lambda_1(Bf)$ is decreasing in B.*

Proof. From the proof of Proposition 5.1, it is easy to show that, if $\displaystyle\int_C f_u(x,0) < 0$, then $\lambda_1(Bf) > 0$ for $B > 0$ small enough, since $\lambda_1(0) = 0$ and, from (5.5), $\left.\frac{d\lambda_1(Bf)}{dB}\right|_{B=0} = -\displaystyle\int_C f_u(x,0) > 0$.

There exists a positive and periodic function ϕ_0 such that

$$\int_C f_u(x,0)\phi_0^2 > 0. \tag{5.7}$$

Then, from (5.2),

$$\lambda_1(Bf) \leq \frac{\displaystyle\int_C \left[\nabla\phi_0 \cdot (A(x)\nabla\phi_0) - Bf_u(x,0)\phi_0^2\right] dx}{\displaystyle\int_C \phi_0^2}. \tag{5.8}$$

Clearly, this shows that $\lambda_1(Bf) < 0$ for B large enough. The concavity of $B \mapsto \lambda_1(Bf)$ and the fact that $\lambda_1(0) = 0$ then imply that $B \mapsto \lambda_1(Bf)$ is decreasing at least when $\lambda_1(Bf)$ is negative, and thus for $B > 0$ large enough. □

5.2 Influence of the "shape" of $f_u(x, 0)$

This section is concerned with the study of the dependence of the first eigenvalue λ_1 of (2.6) on the shape of the function $f_u(x, 0)$. One denotes $\mu(x) = f_u(x, 0)$ and $\lambda_1 = \lambda_1[\mu]$. The following proposition compares the effect of μ and of its average.

Proposition 5.3 *Let μ_0 be a real number. Then*

$$\lambda_1[\mu] \leq \lambda_1[\mu_0], \tag{5.9}$$

whenever $\displaystyle\int_C \mu = \mu_0 |C|$ (where $|C|$ is the Lebesgue measure of the set C).

Proof. From (2.6), replacing $f_u(x, 0)$ by $\mu(x)$, one obtains

$$-\nabla \cdot (A(x)\nabla\phi) - \mu(x)\phi = \lambda_1 \phi = \lambda_1[\mu]\phi, \quad x \in \mathbb{R}^N, \tag{5.10}$$

where $\phi > 0$ is the principal periodic eigenfunction associated to λ_1, with the normalization condition $\|\phi\|_\infty = 1$. Dividing (5.10) by ϕ and integrating by parts over C yields

$$-\int_C \frac{\nabla\phi \cdot (A(x)\nabla\phi)}{\phi^2} - \int_C \mu = \lambda_1 |C| = \lambda_1[\mu]|C|. \tag{5.11}$$

Clearly, clearly, $\phi_{\mu_0} \equiv 1$ and $\lambda_1[\mu_0] = -\mu_0$. Therefore, it follows from equation (5.11) that

$$\lambda_1[\mu] \leq -\frac{\displaystyle\int_C \mu}{|C|} = -\mu_0 = \lambda_1[\mu_0].$$

This completes the proof of Proposition 5.3. □

Proposition 5.4 *Let $\mu_0 \in \mathbb{R}$ and let f be such that $f_u(x, 0) = \mu(x) = \mu_0 + B\nu(x)$, where ν has zero average and $\nu \not\equiv 0$. Let $\lambda_{1,B} = \lambda_1[\mu]$ be the first eigenvalue of (5.10). Then the function $B \mapsto \lambda_{1,B}$ is decreasing in $\mathbb{R}_+$. Furthermore, $\lambda_{1,B}$ is negative for all $B > 0$ if $\mu_0 \geq 0$, and $\lambda_{1,B}$ is negative for $B > 0$ large enough if $\mu_0 < 0$.*

Proof. As in Proposition 5.3, it can be shown that the function $B \mapsto \lambda_{1,B}$ is concave, and $\frac{d\lambda_{1,B}}{dB}\Big|_{B=0} = 0$, $\lambda_{1,0} = -\mu_0$. The conclusion follows as in the proofs of Propositions 5.2 and 5.3. □

Let us now turn out to the effect of rearranging the level sets of μ. We denote by μ^* the function obtained by performing a succession of Steiner periodic rearrangement of μ with respect to the ordered variables $x_1, ..., x_N$ (see Section 2.3.1 above for the definition) .

Proposition 5.5 *Under the above notations, and assuming furthermore that A is the identity matrix, the following inequality holds*

$$\lambda_1[\mu^*] \leq \lambda_1[\mu]. \tag{5.12}$$

Proof. The proof rests on rearrangement inequalities. Let k be a nonnegative real number such that $\mu + k \geq 0$ in $\mathbb{R}^N$, and let ϕ be the principal eigenfunction associated to $\lambda_1[\mu]$, with the normalization condition $\|\phi\|_\infty = 1$.

A classical inequality for rearrangement (Compare e.g. [37]) asserts that:

$$\int_C (\mu + k)^*(\phi^*)^2 \geq \int_C (\mu + k)\phi^2. \tag{5.13}$$

Since $(\mu + k)^* = \mu^* + k$, one infers from (5.13) that $\int_C \mu^*(\phi^*)^2 \geq \int_C \mu\phi^2 + k\int_C [\phi^2 - (\phi^*)^2]$. On the other hand, $\int_C [\phi^2 - (\phi^*)^2] = 0$, whence

$$\int_C \mu^*(\phi^*)^2 \geq \int_C \mu\phi^2. \tag{5.14}$$

Next, it follows from Theorem 2.1 and Remark 2.6 in [37] [3] that

$$\int_C |\nabla\phi|^2 \geq \int_C |\nabla\phi^*|^2. \tag{5.15}$$

As already emphasized, $\lambda_1[\mu^*]$ and $\lambda_1[\mu]$ are given by the following variational formulæ

$$\lambda_1[\mu] = \min_{\psi \in H^1_{per},\ \psi \not\equiv 0} \frac{\int_C \left(|\nabla\psi|^2 - \mu\psi^2\right)}{\int_C \psi^2}, \tag{5.16}$$

[3] see also Berestycki and Brock, *Periodic Steiner symmetrization and applications to some variational problems in cylinders*, paper in preparation, and [9]

and

$$\lambda_1[\mu^*] = \min_{\psi \in H^1_{per},\ \psi \not\equiv 0} \frac{\displaystyle\int_C \left(|\nabla\psi|^2 - \mu^*\psi^2\right)}{\displaystyle\int_C \psi^2}. \tag{5.17}$$

Furthermore, the minimum in (5.16) is reached for $\psi = \phi$. It follows from (5.17) that

$$\lambda_1[\mu^*] \leq \frac{\displaystyle\int_C \left(|\nabla\phi^*|^2 - \mu^*(\phi^*)^2\right)}{\displaystyle\int_C (\phi^*)^2}. \tag{5.18}$$

From (5.14), one has $\displaystyle\int_C \mu^*(\phi^*)^2 \geq \int_C \mu\phi^2$, and, from (5.15), $\displaystyle\int_C |\nabla\phi|^2 \geq \int_C |\nabla\phi^*|^2$. One also knows that $\displaystyle\int_C (\phi)^2 = \int_C (\phi^*)^2$. Finally, it follows from (5.18) that

$$\lambda_1[\mu^*] \leq \frac{\displaystyle\int_C \left(|\nabla\phi|^2 - \mu\phi^2\right)}{\displaystyle\int_C \phi^2} = \lambda_1[\mu], \tag{5.19}$$

and Proposition 5.5 is proved. □

As a conclusion, one can say that from the biological conservation standpoint, among all periodic $\overline{\mu}$ having a given distribution function, the optimal one is necessarily Steiner symmetric, that is, symmetric with respect to $x_i = 0$ and decreasing in x_i, for $x_i \in [0, L_i/2]$ (for each $i = 1, \cdots, N$). Note, however, that the actual optimal shape (among all Steiner symmetric functions in all variables) is not known, even when μ takes only two values.

6 The effect of fragmentation in bounded domain models

The problem of the effects of environment fragmentation on the populations in bounded domains is the main theme of the papers [13, 14, 15] of Cantrell and Cosner. Its biological interest is widely described in this series of papers. In this section, we summarize some properties concerned with the case of bounded domains, and, using a symmetrization argument, we state some general results extending previous works.

Consider the equation

$$u_t - \nabla \cdot (A(x)\nabla u) = f(x,u), \quad x \in \Omega, \tag{6.1}$$

set in a bounded smooth domain $\Omega \subset \mathbb{R}^N$. Assume, say, that the nonlinearity f is smooth and satisfies (2.4-2.5), and that A is a smooth uniformly elliptic matrix field.

For Dirichlet boundary conditions

$$u = 0 \ \text{ on } \partial\Omega,$$

there exists a solution p of

$$\begin{cases} -\nabla \cdot (A(x)\nabla p) = f(x,p), & x \in \Omega \\ p(x) > 0, & x \in \Omega \\ p(x) = 0, & x \in \partial\Omega, \end{cases} \tag{6.2}$$

if and only if the first eigenvalue λ_1 of the operator $\mathcal{L}\phi = -\nabla\cdot(A(x)\nabla\phi) - f_u(x,0)\phi$ in Ω (with Dirichlet boundary conditions on $\partial\Omega$) is negative. Furthermore, if it exists, p is unique.

In the one-dimensional case with constant diffusion du_{xx} and f of the type $f(u) = u - \alpha u^2 - \beta u^2/(1+u^2)$, this result is due to Ludwig, Aronson and Weinberger [40] (see also Murray and Sperb [41] for the two-dimensional case with additional drift terms). It was generalized to any dimension, with a space and density dependent diffusion rate and with a drift term, by Cantrell and Cosner [13, 14], in the case of a nonlinearity f of the type $f(x,u) = m(x)u - c(x)u^2$ (with $c(x) > 0$) .

For the equation (6.2), which has a more general reaction term, the results mentioned above can be proved with the same methods as the ones used in the present paper. Notice that the case of bounded domains is actually much simpler than the periodic case in $\mathbb{R}^N$. In particular, uniqueness of the positive solutions was proved in [4].

Furthermore, using the same arguments as those of section 2.2, the solutions $u(t,x)$ of (6.1) with initial condition $u_0 \geq 0$, $u_0 \not\equiv 0$ converge uniformly in $x \in \overline{\Omega}$ as $t \to +\infty$ to the unique positive solution $p(x)$ if $\lambda_1 < 0$; otherwise, that is if $\lambda_1 \geq 0$, then $u(t,x) \to 0$ uniformly in $x \in \overline{\Omega}$ as $t \to +\infty$ (see also [13, 14, 15, 40] for earlier results in some particular cases).

Some of the above results have been extended by Cantrell and Cosner [16] to some special cases of systems of two equations.

For problem (6.1) in a bounded interval $(0,L)$, the influence of the location of the favourable and unfavourable regions has been studied in [15], on the basis of explicit analytic calculations. This work is restricted to the case of the patch

model, that is when the birth rate $f_u(x,0)$ is piecewise constant and only takes two possible values. For Dirichlet boundary conditions, it is better for species conservation to have the most favourable region concentrated around the middle of the interval, away from the boundary. This kind of problem has also been studied by Harrell, Kröger and Kurata [30], in the case of a two-values patch model. One of the problems analyzed in [30] was the case where the favourable zone, say U, is fixed *a priori*. For a certain class of bounded domains Ω, with Dirichlet boundary conditions, they proved that the position of U that minimized λ_1, was at the "center" (in a certain sense) of Ω. On the contrary, in the case of Neumann boundary conditions, it is better for species conservation to have the favourable and unfavourable regions concentrated near each of the two boundary points of the interval.

Using symmetrization techniques as we did above for the periodic case allows us to extend and much simplify these results. For a general $\mu(x)$, we prove the following:

Theorem 6.1 *Let Ω be a smooth bounded domain of $\mathbb{R}^N$ and assume that Ω is convex in some direction say x_1, and symmetric with respect to $x_1 = 0$. Let μ be continuous in $\overline{\Omega}$ and let $\lambda_1[\mu]$ be the first eigenvalue of*

$$\begin{cases} -\Delta\varphi - \mu(x)\varphi = \lambda_1[\mu]\varphi & \text{in} \quad \Omega \\ \varphi = 0 \quad \text{on} \quad \partial\Omega. \end{cases}$$

Then, $\lambda_1[\mu^*] \leq \lambda_1[\mu]$, where μ^* is the Steiner symmetrization of μ in the variable x_1, with respect to $\{x_1 = 0\}$ and nonincreasing away from $\{x_1 = 0\}$.

Furthermore, equality $\lambda_1[\mu] = \lambda_1[\mu^*]$ holds if and only if μ is symmetric with respect to x_1 and nonincreasing away from $\{x_1 = 0\}$.

In an interval, this theorem provides the optimal rearrangement of a function μ in the sense of finding, among all μ having a given distribution function that function, namely μ^*, that minimizes $\lambda_1[\mu]$. In higher dimensions, this is not known. In dimension $N = 2$ consider the simple patch model when μ is allowed to take two values. When Ω is say a rectangle, then the shape of the optimal μ is not known. From the theorem, we know that it is doubly symmetric in the Steiner sense, hence the favourable zone is connected. However, it is not known that this region is convex, a property which we conjecture holds.

Remark 6.2 When the mean $\int_\Omega \mu = \mu_0$, over a bounded set $\Omega \subset \mathbb{R}^N$, and the upper and lower bounds μ_1 and $-\mu_2$ ($\mu_1, \mu_2 > 0$) of μ are fixed but when the distribution function is not, Cantrell and Cosner [13] have derived the existence of an optimal function $\overline{\mu}$ (that minimizes $\lambda_1(\mu)$), which only takes the two values μ_1 and $-\mu_2$.

If the volume $|\Omega|$ is fixed instead of the shape Ω, under the same assumptions on μ as above, they noted that the optimal function $\overline{\mu}$ was attained when Ω was a ball, and $\overline{\mu} = \mu_1 \chi_E - \mu_2 \chi_{\Omega \setminus E}$, where $E \subseteq \Omega$ is also a ball concentric with Ω. When the distribution function of μ is also imposed, (e.g. when the favourable and unfavourable areas are fixed), we can derive a similar result, using Steiner symmetrizations in any direction. Namely, we obtain that the optimal shape is given by the symmetric and radial decreasing function μ^* having the same distribution function as μ.

Biological interpretation : The result stated in Theorem 6.1 is similar to those of Proposition 2.10 and Theorem 2.11. However, it cannot be connected to spreading phenomena like in infinite domains. The Dirichlet boundary conditions mean that the region outside the domain is immediately lethal. The biological insight of such results is further discussed in [13] and [14].

For Neumann boundary conditions, the situation is more delicate. One has to use *monotone rearrangement*. Consider now the eigenvalue problem :

$$\begin{cases} -\Delta\varphi - \mu(x)\varphi = \Lambda_1[\mu]\varphi & \text{in} \quad \Omega \\ \frac{\partial \varphi}{\partial \nu} = 0 & \text{on} \quad \partial\Omega. \end{cases}$$

Like for the periodic case or for the bounded domain case with Dirichlet condition, the sign of $\Lambda_1[\mu]$ determines the existence of stationary solutions and asymptotic behaviour of the solution of the nonlinear problem (6.1) with Neumann condition.

The monotone rearrangement of a function $v(x)$ of one variable, on an interval (a, b), is defined as the unique monotone (say) nondecreasing function $v^\sharp$ on (a, b) which has the same distribution function as v. Then, define the Steiner monotone rearrangement of a function $v(x_1, \ldots, x_N)$ on a set $\{x\,; x_i \in (a_i, b_i),\ \forall i = 1, \ldots, N\}$, as the function $v^\sharp$ which is obtained from v by performing successive monotone Steiner rearrangements in each of the directions $x_1, \ldots, x_N$.

Theorem 6.3 *Assume that Ω is a cube $\{x\,; x_i \in (a_i, b_i),\ \forall i = 1, \ldots, N\}$. Under Steiner monotone rearrangement, the Neumann eigenvalue satisfies the following inequality : $\Lambda_1[\mu^\sharp] \leq \Lambda_1[\mu]$.*

This theorem rests on the following rearrangement inequality :

$$\int_\Omega |\nabla\varphi|^2 \geq \int_\Omega |\nabla\varphi^\sharp|^2. \tag{6.3}$$

This is well known in dimension 1 (see [37]) but somewhat delicate in dimension N. [4]

[4]This inequality is proved in Berestycki and Brock, *Periodic Steiner symmetrization and applications to some variational problems in cylinders*, paper in preparation.

As a consequence of this result, we see that, in the simplified case of the patch model on a rectangle, the rearranged configuration, where all the favourable patch is concentrated in one of the corners of the domain, leaves better chances of survival than an originally fragmented configuration. An example is given in the figure 4.

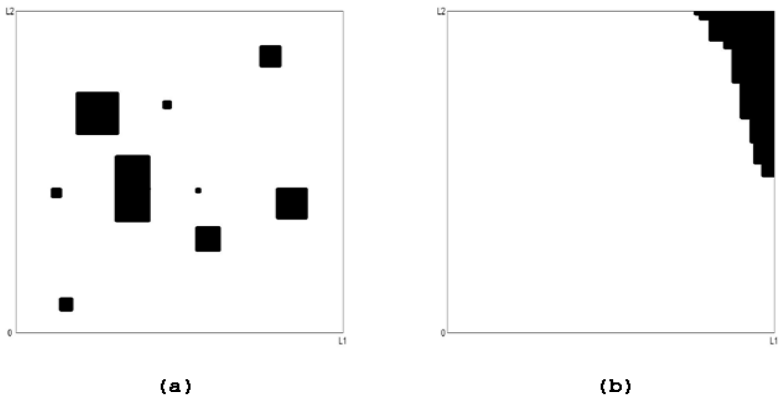

Figure 4: (a) Initial patch, and (b) after monotone Steiner rearrangement

Remark 6.4 As a consequence of this theorem, in the patch case, the optimal rearrangement, under the constraint of a given area of the unfavourable zone, is a μ such that $\mu^\sharp = \mu$. However, like for the other cases, in higher dimension, the question of the optimal shape of the environment (in the patch model) is still open. This appears to be an interesting mathematical question.

Biological interpretation : Neumann conditions mean that the individuals that try to cross the boundary of the domain are immediately rejected inside. In such a case, emigration does not occur. Here, survival is better if the favourable patch is in a corner of the domain. This result sheds light in the context of refuge theory, where a boundary like a fence could have an effect close to that of Neumann boundary conditions.

7 Conclusions

To have a good overview of the mathematical results that we have obtained in this paper, we refer the reader to Section 2. We will summarize here some consequences

from the biological modelling point of view that can be derived from these new results.

As we had mentioned in the introduction, our first aim was to give a complete and rigorous analysis of the *periodic heterogeneous* model of Shigesada and Kawasaki [47] for population dynamics, in any dimension, and with a general reaction term. We established some existence, uniqueness and stability results, which lead to a criterion for the species persistence. It is based on the sign of the first eigenvalue λ_1. Actually, we have shown that, in this model, the condition $\lambda_1 < 0$ is necessary and sufficient for the species to survive. In the case of bounded domains, with various boundary conditions, a similar criterion for "persistence" is discussed in several papers of Cantrell and Cosner [13, 14, 15] (see Section 6). In the case of unbounded domains, with $f(x, s) = \mu(x)s - \nu(x)s^2$, the sufficient part of the condition for existence of a positive steady state also follows from results of Pinsky [44] and Engländer and Kyprianou [20]. These authors actually consider more general operators, not necessarily in the periodic framework.

The quantity λ_1 can be computed empirically, and therefore be used to estimate the suitability of a given environment for some invading species. It carries many informations on the environment and its complex interactions with the species. Thus, in this model, we have succeeded in expressing in a single condition the various complex interactions between diffusion, environment shape and effects leading to persistence or to extinction.

Moreover, we have used this criterion to compare some periodic environments. In particular, we have obtained some results on the effects of fragmentation on species survival. We gave a rigorous proof of the result of Shigesada and Kawasaki [47] for the patch model, which asserts that for a given area of favourable and unfavourable zones, the best environment in terms of species survival is obtained when the unfavourable habitat is regrouped at the center of the periodicity interval (remember that this result, which as been obtained with the help of numerical computations by Shigesada and Kawasaki, concerns the one-dimensional case).

Further, we derived a much more general result. For instance, a consequence of our finding is that assuming a patch model with k types of habitat (including the case $k = 2$ as before), we derive an arrangement of these zones in order to allow better chances for species survival (and that is optimal in the one-dimensional case). The same result holds with an habitat which varies continuously with the space variables. We actually found a symmetric connected rearrangement which is more favourable than the initial disconnected zones.

The optimal shape(s), however, is (are) not known (aside from the one-dimensional case) and this leads to interesting open problems. Nevertheless, owing to our result, one can assert that there exist an optimal rearrangement in which the unfavourable habitat is concentrated in a connected area, at the center of the

periodicity cell. Actually, by changing the periodicity cell, shifting it by half a period in each direction, we prove likewise that chances of survival are increased if it is rather the *favourable* habitat which is concentrated as before. These two formulations are in fact equivalent and the result says really about the effect of fragmentation of the environment.

Further, with Theorem 2.12, we analyzed the effects of high amplitude. One of the results we established here is that, increasing the effective birth rate and the effective death rate in both parts of the environment simultaneously, it suffices to have a very favourable (even quite narrow) zone to allow for species survival, no matter how bad the environment may be elsewhere.

In the course of this paper, four types of "heterogeneity" have been encountered and analyzed. Actually, this term can be misleading since, in each case, an increase of "heterogeneity" does not lead to the same conclusions. First, it has been considered as an uneven way of distributing a given amount of resources on a periodicity cell. Proposition 2.9 asserts that it is better for species survival than an equal repartition of the resource. The idea of "heterogeneity" can also be expressed in terms of "fragmentation", which has been shown, with Proposition 2.10 and Theorem 2.11 to have a negative effect on species survival. Finally, in the biological discussion following Theorem 2.12, we emphasized that increasing the amplitude of the heterogeneity was beneficial whereas increasing the frequency could be detrimental.

All these properties bear consequences for species survival and also shed light on conditions needed to eradicate invading biological species.

The methods which we introduce in this paper using various rearrangements also allow us to extend some results of Cantrell and Cosner [13, 14, 15], and Harrell, Kröger and Kurata [30] in the framework of bounded domains to more general nonlinearities and higher dimensions. Precise results are discussed in Section 6.

The mathematical results of Theorems 2.1, 2.4 and Proposition 3.9, obtained in the case of unbounded domains, will enable us to study spreading phenomena. In a forthcoming paper [7], we analyze the question of invasion for problems of the type (1.3). More precisely, we connect the necessary and sufficient condition for species survival to that for propagation of pulsating fronts invading the uniform state 0 (see [47, 51] for the definition and [5, 6, 33, 50, 51] for some related mathematical results). We further obtain a variational formula for the minimal speed of propagation of such fronts, and we study the influence of the heterogeneity on this speed.

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References

[1] S. Agmon, *Differential equations (Birmingham, Ala., 1983)*, North-Holland Math. Stud. 92, 1984, pp. 7-17.

[2] A.J. Ammerman, L.L. Cavalli-Sforza, *The Neolithic Transition and the Genetics of Populations in Europe*, Princeton Univ. Press, Princeton, NJ, 1984.

[3] D.G. Aronson, H.F. Weinberger, *Multidimensional nonlinear diffusions arising in population genetics*, Adv. Math. **30** (1978), pp. 33-76.

[4] H. Berestycki, *Le nombre de solutions de certains problèmes semi-linéaires elliptiques*, J. Func. Anal. **40** (1981), pp. 1-29.

[5] H. Berestycki, F. Hamel, *Front propagation in periodic excitable media*, Comm. Pure Appl. Math. **55** (2002), pp. 949-1032.

[6] H. Berestycki, F. Hamel, N. Nadirashvili, *The speed of propagation for KPP type problems. I - Periodic framework*, J. Europ. Math. Soc. (2005), to appear.

[7] H. Berestycki, F. Hamel, L. Roques, *Analysis of the periodically fragmented environment model : II - Biological invasions and pulsating travelling fronts*, J. Math. Pures Appl. (2005), to appear.

[8] H. Berestycki, F. Hamel, L. Rossi, *Liouville theorems for semilinear elliptic equations in unbounded domains*, preprint.

[9] H. Berestycki, T. Lachand-Robert, *Some properties of monotone rearrangement with applications to elliptic equations in cylinders*, Math. Nachr. **266** (2004), pp. 3-19.

[10] H. Berestycki, L. Nirenberg, *Travelling fronts in cylinders*, Ann. Inst. H. Poincaré, Anal. Non Linéaire **9** (1992), pp. 497-572.

[11] H. Berestycki, L. Nirenberg, S.R.S. Varadhan, *The principal eigenvalue and maximum principle for second order elliptic operators in general domains*, Comm. Pure Appl. Math. **47** (1994), pp. 47-92.

[12] K. Brown, S.S. Lin, *On the existence of positive eigenfunctions for an eigenvalue problem with indefinite weight function*, J. Math. Anal. Appl. **75** (1980), pp. 112-120.

[13] R.S. Cantrell, C. Cosner, *Diffusive logistic equations with indefinite weights: population models in disrupted environments*, Proc. Roy. Soc. Edinburgh **112** (1989), pp. 293-318.

[14] R.S. Cantrell, C. Cosner, *Diffusive logistic equations with indefinite weights: population models in disrupted environments II*, SIAM J. Math. Anal. **22** (4) (1991), pp. 1043-1064.

[15] R.S. Cantrell, C. Cosner, *The effects of spatial heterogeneity in population dynamics*, J. Math. Biol. **29** (1991), pp. 315-338.

[16] R.S. Cantrell, C. Cosner, *On the effects of spatial heterogeneity on the persistence of interacting species*, J. Math. Biol. **37** (1998), pp. 103-145.

[17] Y. Capdeboscq, *Homogenization of a neutronic critical diffusion problem with drift*, Proc. Royal Soc. Edinburgh **132 A** (2002), pp. 567-594.

[18] S. Cano-Casanova, J. López-Gómez, *Permanence under strong aggressions is possible*, Ann. Inst. H. Poincaré, Anal. Non Linéaire **20** (2003), pp. 999-1041.

[19] L.L. Cavalli-Sforza, M.W. Feldman, *Cultural Transmission and Evolution : A Quantitative Approach*, Princeton Univ. Press, Princeton, NJ, 1981.

[20] J. Engländer, A.E. Kyprianou, *Local extinction versus local exponential growth for spatial branching processes*, Ann. Probab. **32** (2004), pp. 78-99.

[21] J. Engländer, R.G. Pinsky, *On the construction and support properties of measure-valued diffusions on $D \subseteq R^d$ with spatially dependent branching*, Ann. Probab. **27** (1999), pp. 684–730.

[22] J. Engländer, R.G. Pinsky, *Uniqueness/nonuniqueness for nonnegative solutions of second-order parabolic equations of the form $u_t = Lu + Vu - \gamma u^p$ in R^n*, J. Diff. Equations **192** (2003), pp. 396-428.

[23] P.C. Fife, J.B. McLeod, *The approach of solutions of non-linear diffusion equations to traveling front solutions*, Arch. Ration. Mech. Anal. **65** (1977), pp. 335-361.

[24] R.A. Fisher, *The advance of advantageous genes*, Ann. Eugenics **7** (1937), pp. 335-369.

[25] M. Freidlin, *On wavefront propagation in periodic media*, Stochastic analysis and applications, Adv. Probab. Related Topics, **7**, Dekker, New York (1984), pp. 147-166.

[26] M. Freidlin, *Semi-linear PDEs and limit theorem for large deviations*, Springer Lecture Notes in Mathematics **1527**, 1992.

[27] M. Freidlin, *Markov Processes and Differential Equations: Asymptotic Problems*, Lectures in Mathematics ETH Zurich, Birkhauser Verlag, Basel, 1996.

[28] J. Gärtner, M. Freidlin, *On the propagation of concentration waves in periodic and random media*, Sov. Math. Dokl. **20** (1979), pp. 1282-1286.

[29] G.H. Hardy, J.E. Littlewood, G. P'olya, *Inequalities*, Cambridge University Press, Cambridge, 1952.

[30] E.M. Harrell, P. Kröger, K. Kurata, *On the placement of an obstacle or a well so as to optimize the fundamental eigenvalue*, SIAM J. Math. Anal. **33** (1) (2001), pp. 240-259.

[31] P. Hess, *Periodic-parabolic boundary value problems and positivity*, Pitman Research Notes in Mathematics Series, **247**. Longman Scientific & Technical, Harlow, UK, 1991.

[32] D.E. Hiebeler, *Populations on Fragmented Landscapes with Spatially Structured Heterogeneities: Landscape Generation and Local Dispersal*, Ecology **81** (6) (2000), pp. 1629-1641.

[33] W. Hudson, B. Zinner, *Existence of travelling waves for reaction-diffusion equations of Fisher type in periodic media*, In: Boundary Value Problems for Functional-Differential Equations, J. Henderson (ed.), World Scientific, 1995, pp. 187-199.

[34] J. Hughes, *Modeling the effect of landscape pattern on mountain pine beetles*, Thesis, Simon Fraser University, 2002.

[35] V. Hutson, K. Mischaikow, P. Polacik, *The Evolution of dispersal rates in a heterogeneous time-periodic environment*, J. Math. Biol. **43** (2001), pp. 501-533.

[36] J.P. Kaipio, J. Tervo, M. Vauhkonen, *Simulations of the heterogeneity of environments by finite element methods*, Math. Comput. Simul. **39** (1995), pp. 155-172.

[37] B. Kawohl, *On the isoperimetric nature of a rearrangement inequality and its consequences for some variational problems*, Arch. Ration. Mech. Anal. **94** (1986), pp. 227-243.

[38] N. Kinezaki, K. Kawasaki, F. Takasu, N. Shigesada, *Modeling biological invasion into periodically fragmented environments*, Theor. Population Biol. **64** (2003), pp. 291-302.

[39] A.N. Kolmogorov, I.G. Petrovsky, N.S. Piskunov, *Étude de l'équation de la diffusion avec croissance de la quantité de matière et son application à un problème biologique*, Bulletin Université d'État à Moscou (Bjul. Moskowskogo Gos. Univ.), Série internationale **A 1** (1937), pp. 1-26.

[40] D. Ludwig, D.G. Aronson, H.F. Weinberger, *Spatial patterning of the spruce budworm*, J. Math. Biol. **8** (1979), pp. 217-258.

[41] J.D. Murray, R.P. Sperb, *Minimum domains for spatial patterns in a class of reaction-diffusion equations*, J. Math. Biol. **18** (1983), pp 169-184.

[42] R.G. Pinsky, *Positive harmonic functions and diffusion*, Cambridge University Press, 1995.

[43] R.G. Pinsky, *Second order elliptic operators with periodic coefficients: criticality theory, perturbations, and positive harmonic functions*, J. Funct. Anal. **129** (1995), pp. 80-107.

[44] R.G. Pinsky, *Transience, recurrence and local extinction properties of the support for supercritical finite measure-valued diffusions*, Ann. Probab. **24** (1996), pp. 237-267.

[45] S. Senn, *On a nonlinear elliptic eigenvalue problem with Neumann boundary conditions, with an application to population genetics*, Comm. Part. Diff. Equations **8** (1983), pp. 1199-1228.

[46] S. Senn, P. Hess, *On positive solutions of a linear elliptic eigenvalue problem with Neumann boundary conditions*, Math. Ann. **258** (1981/82), pp. 459-470.

[47] N. Shigesada, K. Kawasaki, *Biological invasions: theory and practice*, Oxford Series in Ecology and Evolution, Oxford : Oxford University Press, 1997.

[48] N. Shigesada, K. Kawasaki, E. Teramoto, *Traveling periodic waves in heterogeneous environments*, Theor. Population Biol. **30** (1986), pp. 143-160.

[49] J.G. Skellam, *Random dispersal in theoretical populations*, Biometrika **38** (1951), pp. 196-218.

[50] H. Weinberger, *On spreading speed and travelling waves for growth and migration models in a periodic habitat*, J. Math. Biol. **45** (2002), pp. 511-548.

[51] X. Xin, *Existence of planar flame fronts in convective-diffusive periodic media*, Arch. Ration. Mech. Anal. **121** (1992), pp. 205-233.